UNIVERSITY OF GUELPH
COLLEGE OF BIOLOGICAL SCIENCE
Department of Zoology

GUELPH, ONTARIO, CANADA · N1G 2W1
Telephone (519) 824-4120

Rerum
Cognoscere
Causas

9 November 1982

Dr. Robert J. Behnke
Department of Fishery and Wildlife
Biology
Colorado State Univ.
Fort Collins, Colo. 80523
U.S.A.

Dear Bob:

Here are the reprints you requested in a letter which awaited my return from Europe. I wish Mark lived to see it in print.

... reviewed
- CJFAS
- Nordeng -
solution to charr problem

Is there any hope our Charr Symposium papers will see the light of day? I have now eggs of the rare aurora trout in incubators aiming at distinguishing it that way from the brook's. Futile hope, maybe.

Apropos the greater activity of Russians in the comparative studies on fish development: First of all there was a pre-revolution tradition in morpho-embryologic work, greater than elsewhere, for example, by Wolff, Schmalhausen, Severstov, de Bear, Kazansky. The Soviet activists in that field were (Vosnetsov, Kryzkanovsky) and are (Smirnov, Disler) all students of the tsarist school. As I see it the decline in North America of similar studies, started here by Agassiz, was caused by an overemphasis on quantitative and experimental studies in addition to chance in availability of personalities. The "Marxist-Lysenkoid" phenomenon caused only some misapplication of ideology, e.g. the Marxist version of saltation, to be introduced into already existing activity. (Incidentally, it has nothing to do with our present concept of saltation in ontogeny, except its common historical origin in the Hegelian philosophy). I have written on this topic in two articles presently in print (Plymouth Symposium). Furthermore, the totalitarian state forced researchers to focus on commercially important species or at least to babble about such importance; all of it with little bearing on the developmental content.

...continued...

Summing up, I would not declare the Soviet to cause any greater activity in this field than the field and available scientists would generate anyhow. But, as in other fields, the Soviet ideology (or Lysenko's excesses) caused some unnecessary verbosity and false pretenses to enter developmental papers. Soviet reared youth now produces little of interest even in this field, studies are fewer and standards lower. This alone proves my points.

I will try to attend the January meeting, so we may talk more about it then.

Cordially,

Eugene

EKB:bsa
Encl.

Eugene K. Balon
Professor

CHARRS

Salmonid Fishes of the Genus *Salvelinus*

Edited by

Eugene K. Balon

Perspectives in Vertebrate Science
Series Editor: Eugene K. Balon

Volume 1

1980

Dr. W. Junk bv Publishers
P.O. Box 13713 2501 ES The Hague, The Netherlands

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The feeding mechanism and cephalic myology of *Salvelinus fontinalis*: form, function, and evolutionary significance

George V. Lauder, Jr. & Karel F. Liem

10.1 Introduction

Studies on the feeding mechanics of teleosts have been focused primarily on the advanced teleostean groups (Alexander 1967a, 1967b, Anker 1974, Dutta 1968, 1975, Liem 1967, 1970, 1973, Nyberg 1971, Osse 1969), while relatively little attention has been paid to the more primitive fishes (Kirchhoff 1958, Tchernavin 1948, Vrba 1968). The salmoniforms in particular have been badly neglected; the major study of feeding in this group being that of Tchernavin (1953) who based his analysis on the manipulation of preserved specimens of *Salmo salar* and *Chauliodus sloani*. Ballintijn & Hughes (1966) recorded the activity pattern of respiratory muscles in *Salmo*; Günther & Deckert (1953, 1955) have studied the trophic structures in stomiatoids.

Salmoniform fishes are among the most primitive fishes of the cohort Euteleostei (Greenwood *et al*. 1966, Rosen 1973) and thus form an important link between the other basal teleostean groups (Osteoglossomorpha, Elopomorpha, Clupeomorpha) and higher euteleosteans. A detailed knowledge of the feeding mechanism in generalized salmoniform fishes is thus important, both for a comparative approach to teleostean functional anatomy, and as a major link in the evolution and adaptive radiation of the teleostean feeding apparatus.

The aim of this chapter is to provide a description of the cranial and branchial myology of brook charr, *Salvelinus fontinalis*, to analyze the feeding mechanism with special reference to musculoskeletal interactions within the head during prey capture, and to discuss the form and function of the feeding mechanism in light of actinopterygian jaw evolution.

10.2 Materials and methods

The cranial and branchial myology was described from over twenty specimens of *Salvelinus fontinalis* (Museum of Comparative Zoology (MCZ) 52115; 28 specimens). *Salvelinus alpinus* (MCZ 52443; 3 specimens), *S. namaycush* (MCZ 52576, 52577; 6 specimens), and *S. malma* (MCZ 52445; 3 specimens) were also examined for comparative purposes.

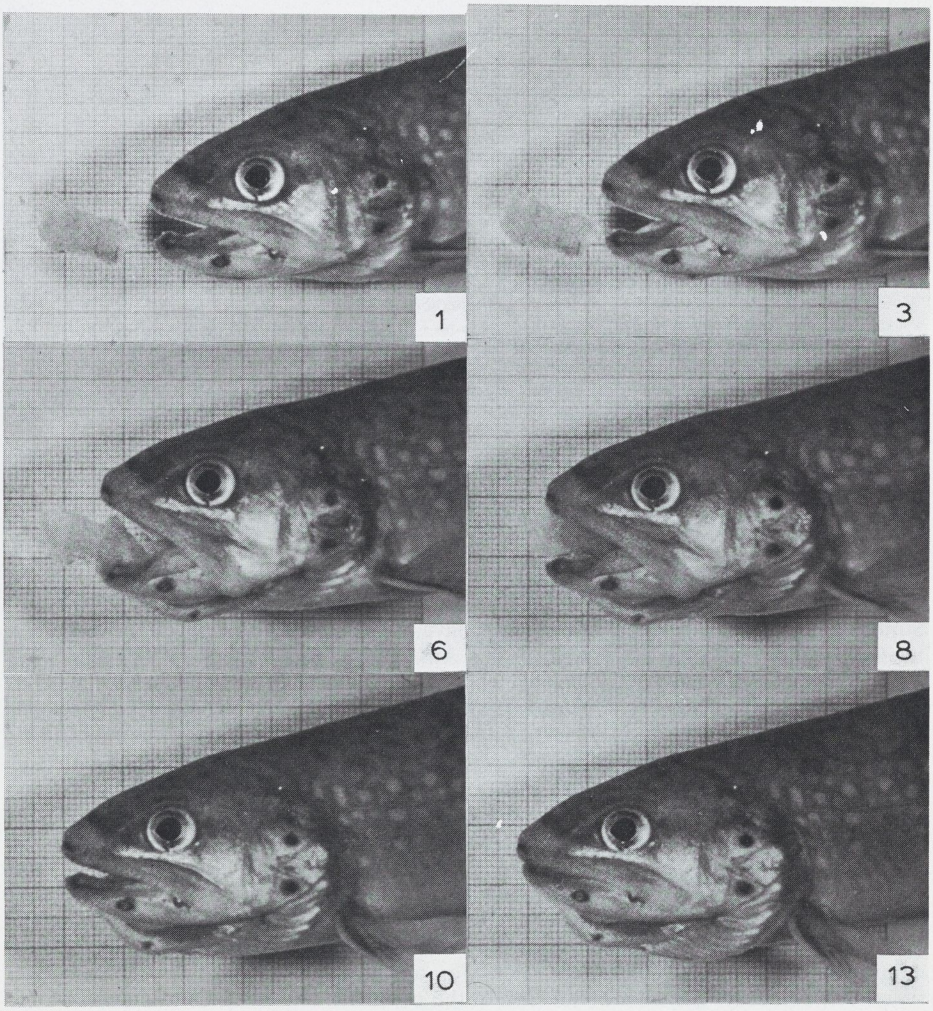

Fig. 1. High-speed cinematography (200 frames sec^{-1}) of feeding *Salvelinus fontinalis* (17.8 cm SL; positive prints of frames 1, 3, 6, 8, 10 and 13 from a feeding sequence. Time between successive frames at 200 frames sec^{-1} is 5 msec. Several of the markers used for cineradiography are visible.

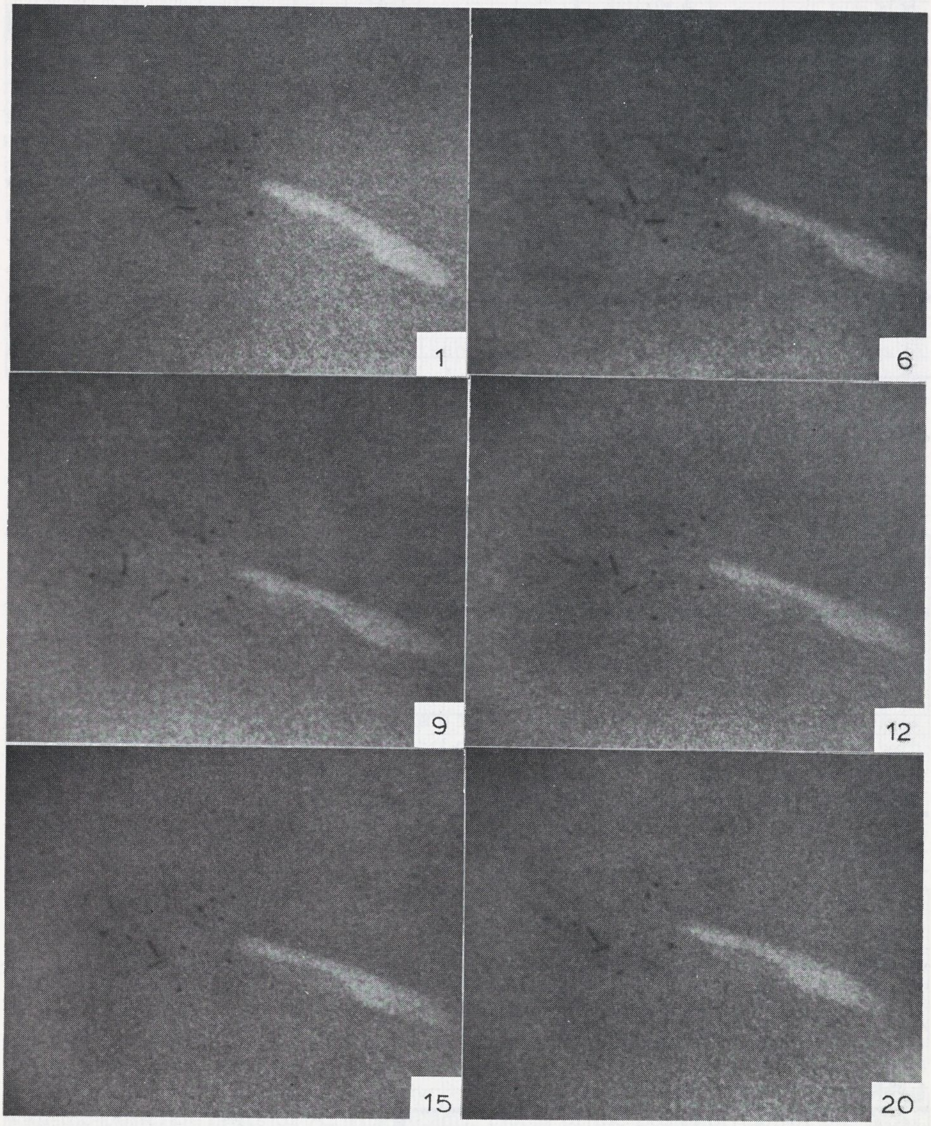

Fig. 2. High-speed cineradiography (200 frames sec^{-1}) of feeding in *Salvelinus fontinalis*; frames 1, 6, 9, 12, 15 and 20 of a feeding sequence. The mouth has closed shortly before frame 15. Small steel screws, lead markers, and pieces of surgical wire have been unilaterally implanted in the bones allowing direct measurement of bone movement during feeding. For a key to the markers see Figure 15. Hyoid depression, maxillary swing, and mandibular depression are most easily seen; note the changing relationship between the maxillary and hyoid wires. The swimbladder is located to the right. The skull bones are not heavily ossified and are not clearly visible in cineradiographic films.

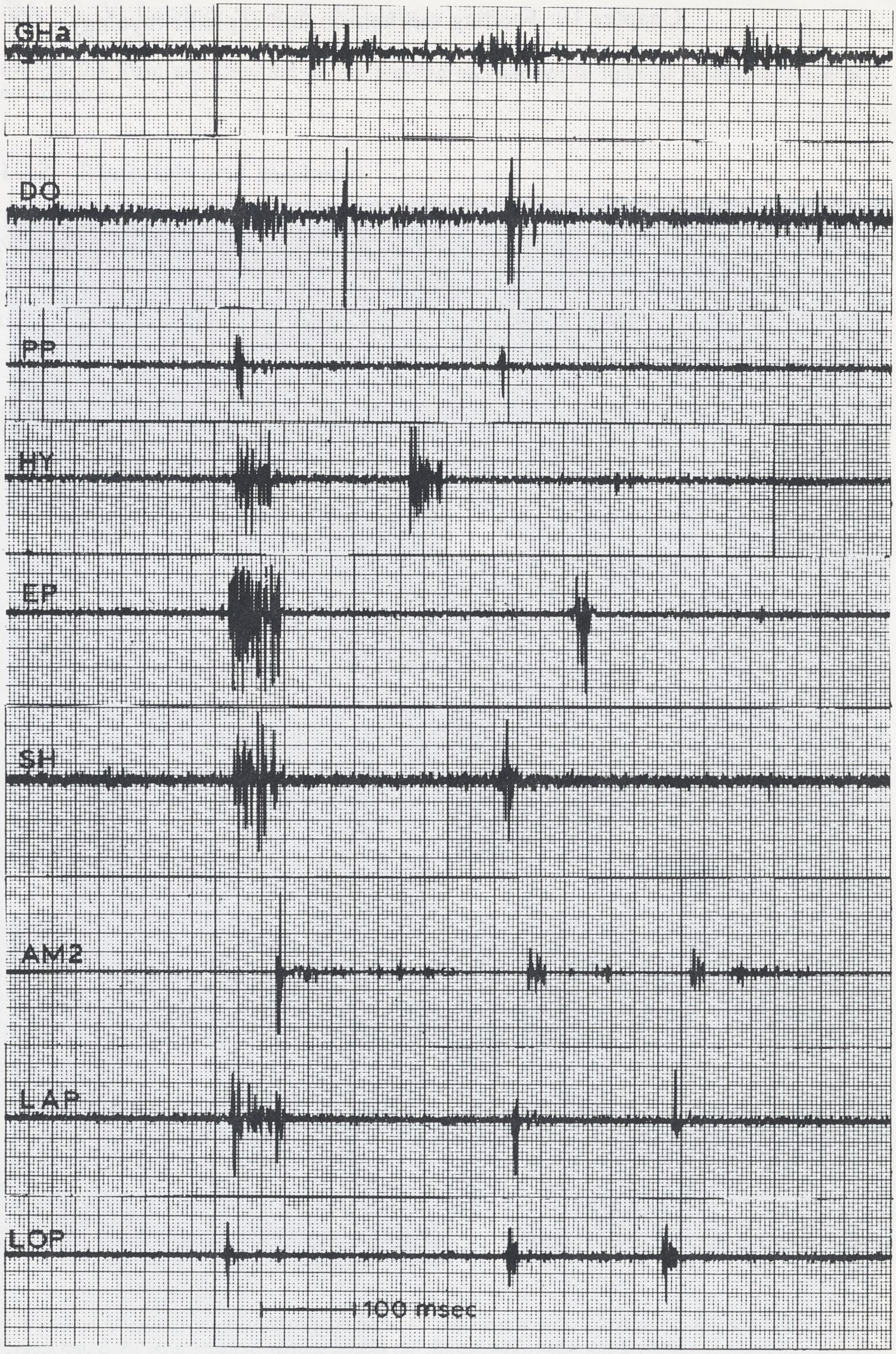

Fig. 3. Electromyograms of nine cranial muscles during feeding in *Salvelinus fontinalis*. The levator operculi and the epaxial muscles are the first muscles to contract during prey capture. Muscles: AM2, second division of the adductor mandibulae; DO, dilator operculi; EP, epaxial muscles; GHa, geniohyoideus anterior; HY, hypaxial muscles; LAP, levator arcus palatini; LOP, levator operculi; PP, obliquus superioris; SH, sternhyoideus.

High-speed cinematography at 200 frames sec^{-1} was used to establish the basic pattern of bone movements during feeding (Fig. 1). A Photosonics 16 mm–1 PL camera was used in conjunction with three 600 W Smith-Victor filming lights and Kodak 4X reversal film.

X-ray cinematography allowed direct measurement of bone movements. Siemens radiographic equipment with a Sirecon image intensifier and an Eclair GV-16 camera yielded cineradiographic film at 200 frames sec^{-1}. Kodak Plus-X reversal film was exposed at 120 mA and 38 and 40 kV. Small jeweler's screws (0.5–1 mm head diameter) and short pieces of surgical wire (0.4 mm in diameter) were implanted under anesthesia in the bones of the head and pectoral girdle several days before filming. The screws and wires appear clearly as points and lines on the film (Fig. 2) and permit the first direct measurement of bone movements during feeding in fishes. No adverse effects from the implantation were noted.

Positive prints of each frame of the feeding sequences were made from the 16 mm films, and the measurements taken from the prints with dial calipers.

Electromyography of the cranial muscles was used to determine the timing of muscle contraction during feeding (Fig. 3). A Brush High-Gain Biomedical Coupler (sensitivity 1 μV $div.^{-1}$) and a Brush 260 chart recorder were coupled to a revolving connector which allowed unrestrained movement of the fish. Fine wire electrodes were implanted in the muscles (Basmajian & Stecko 1962) and supported by a clamp attached to a loop of wire through the epaxial musculature. Electrical potentials were recorded at 37.5 cm sec^{-1} on a Honeywell 5600 tape recorder and played back at 4.7 cm sec^{-1} to facilitate analysis. Activity in five muscles was recorded simultaneously, and the consistently well defined and high amplitude contraction of the levator operculi at the start of the feeding sequence was used as a reference to compare the results of different experiments.

10.3 **Myology of the feeding apparatus**

The cephalic myology of *Salvelinus fontinalis* is described as a prelude to the functional analysis of the feeding mechanism. Our comparative studies have revealed only slight differences in the myology of the different species of *Salvelinus*. Chief interspecific differences in the cephalic myology are proportional ones coupled with only very slight differences in the insertion sites of certain muscles. Thus the description for *Salvelinus fontinalis* is representative for all members of the genus. Several authors have dealt with some aspects of the cephalic myology of *Salmo* (Vetter 1878, Greene & Greene 1913, Van Dobben 1935, Ballintijn & Hughes 1965). In this topographical treatise, we will closely adhere to the nomenclature proposed by Winterbottom (1974).

10.31 *Muscles of the cheek*

Adductor mandibulae (Fig. 4, 6, 10:am). As in most primitive teleosts, the adductor mandibulae muscle is divided into two parts: A_2A_3 and A_w, both of which are innervated by branches of the ramus mandibularis of the trigeminal nerve. Part A_2A_3 occupying the ventrolateral region of the cheek (Fig. 4:am) originates from the hyomandibular, preopercular, metapterygoid, symplectic and quadrate. Anteroventrally the fibers of the anterior part of A_2A_3 pass medially to the coronoid process sharing a distinct myocomma with the posterior fibers of A_w (Fig. 6:am). Fibers of the posterior half of the A_2A_3 complex converge on a well differentiated elongate tendon, which runs along the posterior edge of the A_w muscle to insert in the Meckelian fossa anterior to the quadratomandibular joint (Fig. 6). Thus the insertion of the A_2A_3 complex is effectively in the Meckelian fossa via the A_w muscle and the elongate tendon.

The A_w part of the adductor mandibulae, often called the intramandibularis, attaches to the Meckelian fossa on the medial aspect of the mandible. The fibers of the A_w part arise from the myocomma of the A_2A_3 complex and run from an anteroventral to a posterodorsal direction.

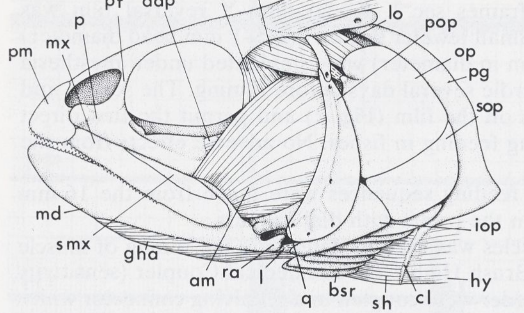

Fig. 4

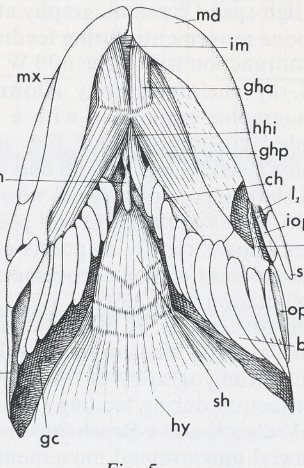

Fig. 5

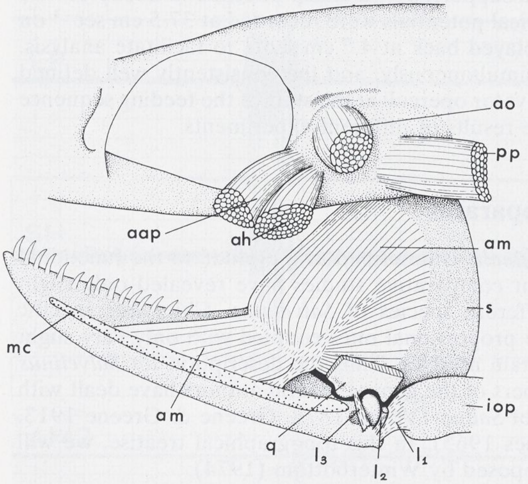

Fig. 6

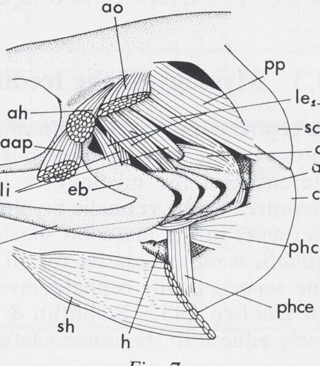

Fig. 7

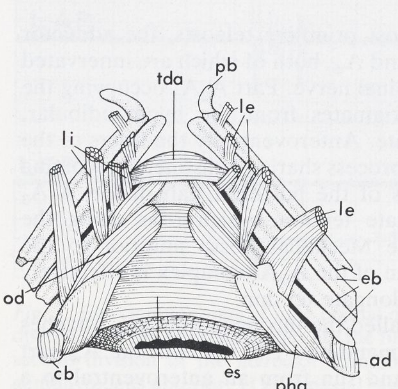

Fig. 8

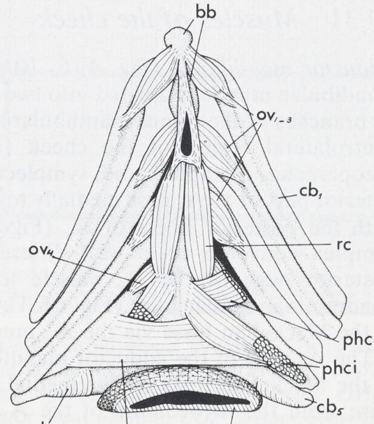

Fig. 9

Levator arcus palatini (Fig. 4, 10:lap). This muscle occupies the back part of the orbit between the skull and the suspensory apparatus and is innervated by the maxillo-mandibularis branch of the trigeminal nerve and by a major branch of the facial nerve (Meijer 1975). The muscle is conical, with the apex as its fleshy origin from the sphenotic. From this dorsalmost position, the fibers pass posteroventrally to insert musculously on the lateral aspects of the hyomandibular and metaptergyoid. Common synonyms for this muscle are levator hyoidei, levator hyomandibulae et arcus palatini, and protractor hyomandibularis.

Dilator operculi (Fig. 4, 10:do) lies posterior to the levator arcus palatini and is innervated by the maxillo-mandibularis branch of the trigeminal nerve and by a branch of the facial motor nerve (Meijer 1975). Although it is immediately adjacent to the levator arcus palatini, its fibers are clearly separated. From its fleshy origin within the shallow dilator fossa located in the sphenotic and frontal bones, the fibers run posteroventrally converging on a tendon of insertion, which is attached to an earlike process of the opercular (Fig. 4:op). A common synonym for the muscle is dilatator operculi.

Levator operculi (Fig. 4, 10:lo). Just behind the dilator operculi, lies a clearly separated levator operculi muscle, which is innervated by the ramus hyomandibularis of the facial

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Fig. 4. Left lateral view of superficial cephalic muscles of *Salvelinus fontinalis*. Abbreviations: AAP, adductor arcus palatini; AM, adductor mandibulae A_2A_3; BSR, branchiostegal ray; CL, cleithrum; DO, dilator operculi; EP, epaxial muscles; GHA, geniohyoideus anterior; IOP, interopercular; HY, hypaxial muscles; L, interoperculomandibular ligament; LAP, levator arcus palatini; LO, levator operculi; MD, mandible; MX, maxilla; OP, opercular; P, palatine; PF, prefrontal; PG, pectoral girdle; PM, premaxilla; POP, preopercular; Q, quadrate; RA, retroarticular process; SH, sternohyoideus; SMX, supramaxilla; SOP, subopercular.

Fig. 5. Superficial aspect of ventral cephalic muscles of *Salvelinus fontinalis*. Left side has been spread apart to reveal ligaments. Abbreviations: BSR, branchiostegal ray; CH, ceratohyal; GC, gill cavity; GHA, geniohyoideus anterior; GHP, geniohyoideus posterior; HHI, hyohyoideus inferior; HY, hypaxial muscles; IM, intermandibularis; IOP, interopercular; L_1, interoperculomandibular ligament; L_2, mandibulohyoideum ligament; MD, mandible; MX, maxilla; OP, opercular; SH, sternohyoideus; SOP, subopercular; UH, urohyal.

Fig. 6. Medial aspect of right adductor mandibulae muscle complex after removal of the right palatopterygoid complex with intact right preopercular(s) and partially removed right quadrate (q). Neurocranium viewed from left lateral aspect with associated muscles. Abbreviations: AAP, adductor arcus palatini; AH, adductor hyomandibulae; AM, adductor mandibulae: upper part is $A_{2,3}$ and lower part is A_w; AO, adductor operculi; IOP, interopercular; L_1, interoperculomandibular ligament; L_2, mandibulohyoideum ligament; L_3, medial collateral ligament; MC, Meckel's cartilage; PP, protractor pectoralis; Q, quadrate; S, suspensorium.

Fig. 7. Lateral view of the branchial muscles of *Salvelinus fontinalis*, with other muscles associated with the neurocranium and pectoral girdle. Left opercular series, hyoid ramus, suspensory apparatus, gill filaments and gill rakers removed. Abbreviations: AAP, adductor arcus palatini; AD, adductor; AH, adductor hyomandibulae; AO, adductor operculi; cb, first ceratobranchial 1–5; CL, cleithrum; EB, first epibranchial; H, heart; LE 1–4, levatores externi 1–4; LI, levatores interni; OD, obliquus dorsalis; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; PP, olbiquus superioris; SCL, supracleithrum; SH, sternohyoideus.

Fig. 8. Dorsal view of the branchial basket and its musculature of *Salvelinus fontinalis* after removal of gill filaments. Abbreviations: AD, adductor; CB, fifth ceratobranchial; EB, epibranchials 1–4; ES, esophagus; LE, levatores externi; LI, levatores interni; OD, obliquus dorsalis; PB, pharyngobranchial; PHA, obliquus posterior; TDA, transversus dorsalis anterior; TDP, transversus dorsalis posterior.

Fig. 9. Ventral view of the branchial basket and associated muscles of *Salvelinus fontinalis* after removal of gill filaments and the right pharyngocleithralis internus muscle. Abbreviations: BB, basibranchial; CB_1, first ceratobranchial; CB_5, fifth ceratobranchial; ES, esophagus; OV_{1-3}, obliqui ventrales 1–3; OV_4, obliquus ventralis 4; PHA, obliquus posterior; PHCE, pharyngocleithralis externus; PHCI, pharyngocleithralis internus; RC, rectus communis; TVA, transversus ventralis.

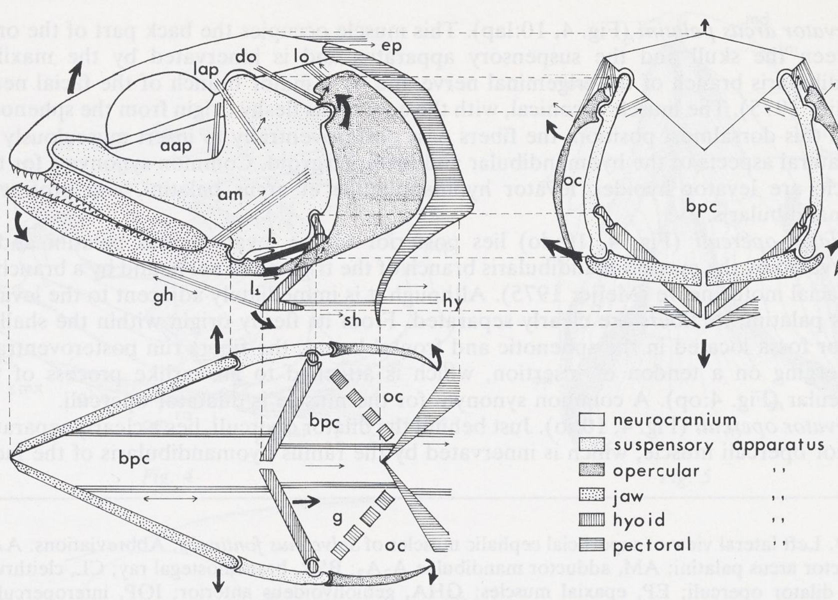

Fig. 10. Three-dimensional diagram of the major mechanical units, muscles and ligaments of the head of brook charr. Muscles and the principal direction of their forces are indicated respectively by light lines and light arrows. Heavy arrows depict major movements during the expansive phase of the feeding cycle. Ligaments (L_1 interoperculomandibular; L_2, mandibulohyoideum) are black. Abbreviations: AAP, adductor arcus palatini; AM, adductor mandibulae; BPC, buccopharyngeal cavity; DO, dilator operculi; EP, epaxial muscles; G, gills; HY, hypaxial muscles; L_1, interoperculomandibular ligament; L_2, mandibulohyoid ligament; LAP, levator arcus palatini; LO, levator operculi; oc, opercular cavity; SH, sternohyoideus.

nerve. Ballintijn & Hughes (1965) claim that this muscle is not separate from the adductor operculi. Our observations on *Salvelinus* and *Salmo* show that the fibers of the levator operculi are distinctly discontinuous with those of the adductor operculi. Both the origin from the pterotic and insertion on the dorsal and dorsomedial face of the opercular are musculous. The straplike muscle is parallel fibered and not subdivided.

Adductor arcus palatini (Fig. 4, 6, 7, 10:aap). This conical muscle forms the posterior floor of the orbit between neurocranium and suspensorium. As is the case for all derivatives of the constrictor hyoideus dorsalis, this muscle is innervated by the ramus hyomandibularis of the facial nerve. Both the origin from the prootic and insertion on the metapterygoid and hyomandibular are musculous. As in all basal teleosts, the muscle is restricted to the posterior part of the orbital cavity, but its fibers are clearly separated from those of the adductor hyomandibulae and adductor operculi (Fig. 6:aap, ah, ao).

Adductor hyomandibulae (Fig. 6:ah). Closely associated with the adductor arcus palatini is the adductor hyomandibulae, which is also innervated by the ramus hyomandibularis of the facial nerve. Its topographical features seem to indicate that this muscle has separated from the posterior region of the adductor arcus palatini. Both muscles share a musculous origin from the prootic, but the fleshy insertion of the conical adductor hyomandibulae is restricted to the posterodorsomedial aspect of the hyomandibular. The muscle is more commonly known as the adductor hyomandibularis.

Adductor operculi (Fig. 6:ao). This short almost cylindrical muscle runs from the dorsomedial aspect of the opercular to the otic region of the neurocranium. It shares the same innervation, i.e. the ramus hyomandibularis of the facial nerve, with the adductor arcus palatini, adductor hyomandibulae and the levator operculi muscles. Both the origin from the prootic and pterotic, and the insertion on the medial aspect of the opercular just behind the operculohyomandibular joint are musculous. The fiber pattern is essentially parallel.

10.32 *Ventral muscles of the head*

Intermandibularis (Fig. 5:im). This is the most anterior ventral cephalic muscle, innervated by the ramus mandibularis inferior of the trigeminal nerve. Its parallel fibers run transversely between the halves of the mandible. The muscle lies dorsal to the sites of attachments to the dentaries of the geniohyoideus anterior muscles.

Geniohyoideus (Fig. 4, 5:gha, ghp). This parallel-fibered muscle connects the mandible with the hyoid arch. Anteriorly, its left and right halves approximate one another very closely. At the point of approximation is a distinct myocomma. The geniohyoideus anterior (that part anterior to the bifurcation and myocomma) attaches to the inner side of the dentary near the symphysis ventral to the intermandibularis muscle. The geniohyoideus posterior (Fig. 5:ghp) bifurcates to attach to the lateral aspect of the ceratohyal. None of the fibers of the geniohyoideus attach to any branchiostegal ray. As shown by Meijer (1975) the geniohyoideus posterior possesses a double innervation, both by the trigeminal and facial nerves, while the geniohyoideus anterior is innervated by the ramus mandibularis inferior of the trigeminal nerve. The combined muscle complex of geniohyoideus anterior and posterior is more commonly called the protractor hyoidei or protractor hyoideus. We do not use the functional name, since protraction of the hyoid is only one of the functions of the muscle complex. Yet, the name geniohyoideus is not satisfactory either, since this muscle in teleosts is not homologous with the geniohyoideus of tetrapods.

Hyohyoidei abductores (Fig. 5:hhi). These relatively small conical muscles are associated with the first branchiostegal rays. The fibers arise tendinously from the ventral hypohyal and are innervated by the ramus hyoides of the facial nerve. The muscle is more commonly known as the hyohyoideus or the hyohyoideus inferior.

Sternohyoideus (Fig. 4, 5, 7, 10:sh). This cone-shaped muscle is thickened posteriorly and connects the hyoid arch to the pectoral girdle. Right and left halves are fused in the midline. Its innervation is derived from branches of the occipito-spinal nerves, although involvement of the vagus nerve is possible (Meijer 1975). The fibers originate musculously from the cleithrum and converge to insert on the urohyal. Three myocommata are clearly differentiated. It is customary to define the posterior limit of the muscle at the third myocomma. Frequently used synonyms are cleithrohyoideus and rectus cervicis.

10.33 *Dorsal muscles of the branchial basket*

Among this category we can recognize muscles having both sites of attachment on the brancheal arches themselves (*i.e.* intrinsic) and those having one of the attachment sites on the neurocranium (*i.e.* extrinsic). Extrinsic muscles are the four external and two internal levators. As in most primitive teleosts the levator posterior and the retractor dorsalis are lacking. Intrinsic muscles are the obliquus posterior, obliquus dorsalis, transversus dorsalis anterior, transversus dorsalis posterior and the adductores.

Levator externus (Fig. 7, 8:le). Four levatores externi connect the neurocranium to the epibranchials and are innervated by posttrematic branches of the glossopharyngeal and vagus nerves. Fleshy origins of the parallel-fibered straplike muscles are from the prootic, while the tendinous insertions are on the dorsolateral aspects of the epibranchials of the first four arches. The tendon of the fourth levator externus inserts on the fourth epibranchial at a site posterior to the attachment of the fourth obliquus dorsalis. Synonyms for these muscles are levatores arcuum branchialium, levatores arcuum branchialium externi, and levator externus arcus branchialis.

Levator internus (Fig. 7, 8:li). Two relatively small levatores interni run between the prootic and the dorsal surfaces of the second and third infrapharyngobranchials. The innervation is similar to that of the externi. The more anterior parallel-fibered straplike muscle passes in between the transversus dorsalis anterior and the anterolateral margin of the obliquus dorsalis III to insert tendinously on the dorsal aspect of the second infrapharyngobranchial. A hiatus between the posterior margin of the obliquus dorsalis III and the lateral margin of the obliquus dorsalis IV allows the tendon of the spindle-shaped posterior levator internus to attach to the dorsal aspect of the third infrapharyngobranchial. Synonyms for this muscle are levatores arcuum branchialium, levatores arcuum branchialium interni, and levatores interni arcuum branchialium.

Obliquus dorsalis (Fig. 7, 8:od). Two spindle-shaped obliqui dorsales III and IV run between the epi- and infrapharyngobranchials of respectively the third and fourth arches. Both muscles are innervated by branches of the vagus nerve. Origins and insertions are fleshy. Common synonyms include obliquus dorsalis inferior and obliquus dorsalis superior.

Obliquus posterior (Fig. 8:pha). A distinct obliquus posterior muscle connects the posteromedial margin of the fifth ceratobranchial to the extensive posteromedial aspect of the fourth epibranchial and is innervated by the vagus nerve. In contrast to other lower teleosts, the large, parallel-fibered muscle can be distinguished easily from the fifth adductor (Fig. 7:ad, pha). A commonly used synonym is the pharyngoarcualis.

Adductor (Fig. 7, 8:ad). The adductores are small muscles interconnecting the epibranchial and ceratobranchial. The fifth adductor is a short, but relatively stout muscle connecting the posterolateral corner of the epibranchial to the posterodorsal tip of the fifth ceratobranchial. The muscle is located just lateral to the obliquus posterior. A small fourth adductor lies on the medial aspect of the fourth arch, while adductores 1–3 are wanting. All adductores are innervated by the posttrematic branch of the vagus nerve serving the arch in question. The muscles are more commonly known as adductores arcuum branchialium and attractores arcuum branchialium.

Transversi dorsales (Fig. 8:tda, tdp). Two transversi dorsales are present, both of which are innervated by branches of the vagus nerve. Both muscles interconnect the dorsal elements of the branchial arches across the midline. The transversus dorsalis anterior (Fig. 8:tda) interconnects the epibranchials of the second arch, while the transversus dorsalis posterior (Fig. 8:tdp) interconnects the fourth epibranchials. Posteriorly the fibers of the transversus dorsalis posterior become continuous with those of the sphincter oesophagi.

10.34 *Ventral muscles of the branchial basket*

Salvelinus possesses four obliqui ventrales, tranversi ventrales on the fourth and fifth arches, a rectus communis, and pharyngocleithralis externus and internus.

Obliquus ventralis (Fig. 9:ov). Spanning the joints between the ventral surfaces of the hypobranchial and ceratobranchial elements of the first four arches are the spindle-shaped obliqui ventrales muscles, innervated by the posttrematic branch of the vagus nerve. All obliqui ventrales muscles possess tendinous origins and insertions.

Transversus ventralis (Fig. 9:tv). Located posteriorly on the branchial basket are the transversi ventrales muscles, the fibers of which run uninterruptedly across the midline between the ceratobranchials. The attachment to the ceratobranchials is musculous. The major component runs between the fourth ceratobranchials, while a second part spans the gap between the fifth ceratobranchials.

Rectus communis (Fig. 9:rc). As in most basal teleosts, the rectus communis of *Salvelinus* connects the ventral aspect of the third hypobranchial to the anteromedial tip of the fifth ceratobranchial. It is a parallel-fibered, somewhat spindle-shaped muscle with tendinous attachments to the bones. Common synonyms are pharyngohyoideus, pharyngoarcualis and subarcualis rectus communis.

Pharyngocleithralis externus (Fig. 7, 9:pce). This muscle originates from the lateral aspect of the anteroventral region of the cleithrum. Its parallel fibers run straight dorsally to insert on the anteroventral region of the fifth ceratobranchial. Its insertion is medial to the rectus communis but lateral to the pharyngocleithralis internus muscle.

Pharyngocleithralis internus (Fig. 7, 9:pci). This muscle originates musculously from the anterior aspect of the cleithrum. Its fibers run anteriorly and converge to a tendinous insertion on the fifth ceratobranchial. Both the pharyngocleithralis internus as well as the externus are innervated by branches of the spinal nerves. These muscles are better known respectively as the pharyngoclavicularis externus and internus.

10.35 *Miscellaneous muscles*

Under this admittedly inappropriate heading we present brief descriptions of two muscles which play an important role in the biomechanic and electromyographic profiles of the feeding function.

Epaxial muscles (Fig. 4,10:ep). This muscle mass represents the dorsal complex of the body musculature. It passes anteriorly to insert musculously on the dorsal and posterior surfaces of the neurocranium. The more ventral parts of the muscle insert on the supracleithrum and cleithrum. Joining the epaxial muscles are fibers of the obliquus superioris component of the hypaxial body musculature. These fibers fuse with the ventral fibers of the epaxial muscle to insert on the posterolateral aspect of the otic region of the neurocranium.

Hypaxial muscles (Fig. 4, 5, 10:hy). Anteriorly the obliquus superioris and inferioris components of the hypaxial muscles insert on the posterior aspects of the cleithrum and coracoid. Ventrolaterally the superficial fibers pass lateral to the cleithrum and become continuous with the posterolateral part of the sternohyoideus.

10.4 **Key ligaments**

It is beyond the scope of this study to furnish a comprehensive review of the ligaments and arthrology. Instead we offer a brief account of just two ligaments that play a paramount role in the feeding mechanism.

Mandibulohyoideum ligament (Fig. 5, 6, 10:l_2). This ligament connects the medial aspect of the prominent retroarticular process of the mandible with the epihyal of the hyoid arch. Its attachment to the posterodorsolateral aspect of the epihyal just below the joint with the interhyal is quite a bit broader than the attachment to the retroarticular process. As the ligament passes anteriorly, its shape changes from a flat and broad profile, to a rounded one (Fig. 5, 6:l_2). Verraes (1977) has shown that the mandibulohyoideum ligament is present at hatching, and becomes functional at the onset of the eleutheroembryonic phase playing a key role in respiration and jaw opening.

Interoperculomandibular ligament (Fig. 5, 6, 10:l_1). This flat but stout ligament connects the anterior border of the interopercular with the posteroventral corner of the retroarticular process of the mandible. As shown by Verraes (1977) this ligament develops late during the period of active feeding. In contrast to the mandibulohyoideum ligament, the interoperculomandibular ligament is present in all adult teleosts.

10.5 **Functional anatomy of feeding**

10.51 *Basic model of the jaw apparatus*

The head of teleost fishes may be divided into a series of mechanical units (Gans 1969), elements of the head which show little or no internal movement and act as a structural and kinetic unit. There are six such units in the head of charrs: (1) the neurocranium and premaxilla, (2) the maxilla, (3) the mandible, (4) the suspensorium, (5) the two hyoid bars forming the hyoid arch, and (6) the opercular series. In addition, the pectoral girdle is composed of three units: (1) the posttemporal, (2) the supracleithrum, and (3) the cleithrum. The pectoral girdle is not considered as a single mechanical unit since each of the three bones is capable of some movement relative to the others. This proposal is corroborated by cineradiographic films of the pectoral girdle movement during feeding (see later).

These mechanical units are linked to each other by connective tissue or ligaments, and in conjunction with muscles and tendons form musculoskeletal couplings (Liem 1967, 1970) producing relatively well defined movements of the jaw apparatus.

In brook charr at least four major musculoskeletal couplings exist that are directly associated with feeding. The epaxial muscles-neurocranium coupling acts to raise the neurocranium dorsally during the feeding sequence. The lower jaw may be depressed through one or more of several couplings; the levator operculi-opercular series-mandible coupling (Fig. 10:l_1, lo), the sternohyoideus-hyoid apparatus-mandible coupling mediated by the mandibulohyoid ligament (Fig. 10:l_2) and a coupling involving the sternohyoideus-hyoid apparatus-geniohyoideus-mandible (= cleithrum-hyoid-mandible) and possibly connective tissue between the hyoid and lower jaw.

Other less complex couplings mediate movement of the suspensory apparatus and pectoral girdle. [Liem (1970) has considered the branchial musculoskeletal couplings.]

10.52 *Movements of the jaw apparatus and electromyographic profile during feeding*

10.521 *General pattern*

The pattern of muscle activity during feeding in *Salvelinus* shows significant variations within the general plan common to all feeding sequences observed. In certain muscles (Fig. 11:GHa, SH, AM2, LAP, LOP) two main patterns are distinguishable. The A-type feeding sequences involve feeding on food (usually one cm^3 piece of smelt) located on the bottom. The time sequence of events from the start of levator operculi contraction to the onset of adductor mandibulae activity is much longer (105 msec) than in B-type feeding (50 msec). B-type feeding is much more rapid and the time sequence is compressed producing more overlap in muscle activity. B-type patterns are produced when feeding occurs in mid-water on pieces of smelt or when feeding on live fish.

Mid-water feeding sequences are initiated by a well defined, high amplitude contraction of the levator operculi occurring nearly synchronously with hypaxial and epaxial muscle contraction (Fig. 11: LOP, EP, HY). Secondary bursts of activity in the levator operculi do not occur. About 5 msec after the start of levator contraction, the sternohyoideus and levator arcus palatini become synchronously active. The adductor mandibulae starts contracting 50 msec after the onset of activity in the levator operculi, immediately after cessation of sternohyoideus and levator arcus palatini contraction (Fig. 11:AM2, SH, LSP).

In sharp contrast, the A-type feeding sequences show a more variable pattern of muscle activity, the levator operculi and sternohyoideus in particular often showing multiple activity periods within the first 150 msec. Electrical activity in the jaw adductor is not observed until 55 msec later than in B-type feeding. At no time was any activity recorded in either the anterior or posterior portions of the geniohyoideus during the initial strike at the prey.

Although for certain muscles the general pattern and relative timing of activity remains relatively constant within each feeding category in spite of a compression of the time frame, other muscles show considerable variation in the activity period (Fig. 12:HY). This variation could not be correlated with the position of the food or the type of prey. There is relatively little variation in the timing of sternohyoideus contraction relative to the levator operculi but the hypaxial muscles vary greatly both in the onset and duration of activity. In all cases, however, the initial contraction of the hypaxial muscles precedes that of the sternohyoideus (Fig. 12).

The epaxial musculature normally initiates a strong contraction exactly synchronously with the levator operculi but in some cases activity may slightly precede that of the levator

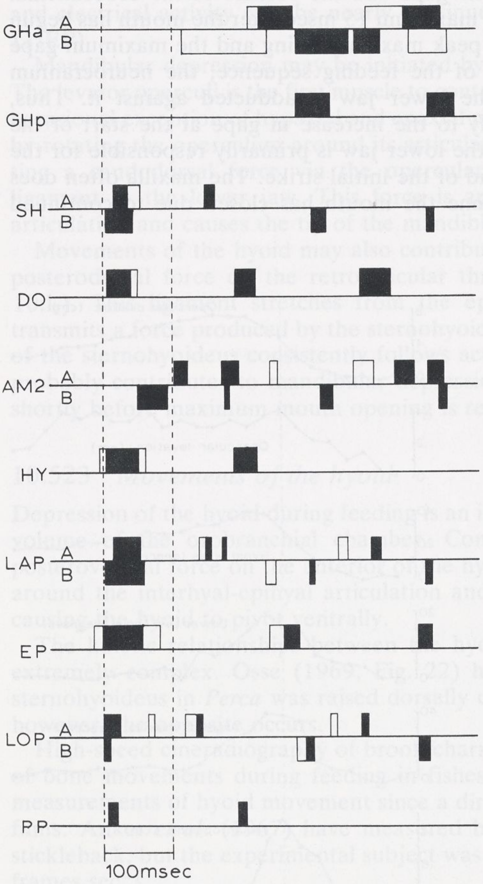

Fig. 11

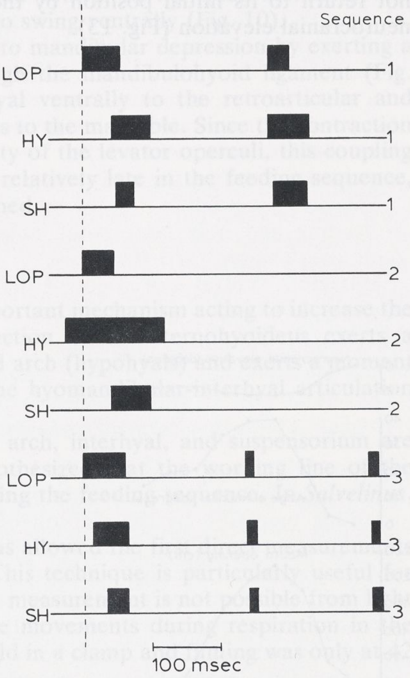

Fig. 12

Fig. 11. Diagram of electromyographic (EMG) recordings of muscle activity in ten cranial muscles of *Salvelinus fontinalis* during the strike at the prey and the first stages of chewing and swallowing. Open blocks indicate frequent variations in the activity pattern. The double EMG record for five muscles, labeled A and B, indicates the two general patterns of muscle activity during feeding in these muscles. B-type activity occurred during rapid mid-water strikes while A-type activity occurred in feeding from the bottom. The first dashed line indicates the onset of levator operculi contraction. Muscles: AM2, second division of the adductor mandibulae; DO, dilator operculi; EP, epaxial muscles; GHa, and GHp, anterior and posterior divisions of the geniohyoideus; HY, hypaxial muscles; LAP, levator arcus palatini; LOP, levator operculi; PP, obliquus superioris; SH, sternohyoideus.

Fig. 12. Diagram of variations in the timing of hypaxial and sternohyoideus muscle activities relative to the levator operculi during the initial stages of feeding in *Salvelinus fontinalis*. The three muscles within each of the three feeding sequences were recorded simultaneously. The dashed line indicates the onset of levator operculi contraction.

operculi. The variability in epaxial muscle contraction time and duration is much less than that observed for the hypaxial muscles.

10.522 *Movement of the neurocranium, maxilla, and mandible*

Elevation of the neurocranium during feeding is an extremely important aspect of the feeding mechanism and acts to increase the gape and the volume of the orobranchial chamber. Neurocranial elevation reaches a maximum 15 msec after the mouth has begun to open and is correlated temporally with peak maxillary swing and the maximum gape between the jaws (Fig. 11). At the end of the feeding sequence, the neurocranium remains in an elevated condition and the lower jaw is adducted against it. Thus, neurocranial movements contribute greatly to the increase in gape at the start of the feeding sequence, but rapid adduction of the lower jaw is primarily responsible for the decrease in mouth opening towards the end of the initial strike. The maxilla often does not return to its initial position by the time the mouth has closed due to continued neurocranial elevation (Fig. 13).

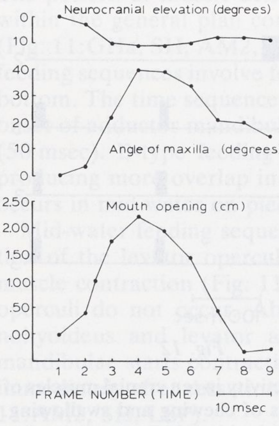

Fig. 13

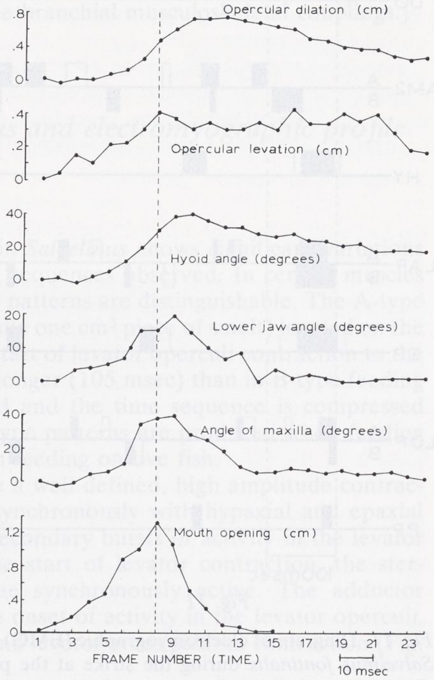

Fig. 14

Fig. 13. Graphic representation of neurocranial elevation, maxillary swing, and mouth opening during feeding in *Salvelinus fontinalis*. The initial value is set equal to zero, and all subsequent changes are recorded as a deviation from zero.

Fig. 14. Graphic representation of bone movements during feeding in *Salvelinus fontinalis* measured from successive frames of a cineradiographic film. Opercular dilation was measured by the change in distance between the interopercular point and the cleithral point (see Fig. 15). This distance increases as the operculum is abducted. Opercular levation was measured by the change in distance of a perpendicular line from the dorsal opercular point to the line representing the vertebral axis. All angles are measured relative to the vertebral axis. Changes in value were measured relative to the initial measurement which was set equal to zero. The dashed line represents the point of maximum gape.

Although the maxilla swings anteriorly through an angle of 40° and is temporally correlated with both mandibular depression and neurocranial elevation, experiments on *Salmo gairdneri* (Lauder 1979) in which the maxillomandibular ligament has been bilaterally removed suggest that the correlation with mandibular depression is spurious. Removal of the maxillomandibular ligament in *Salmo* resulted in an increased angular swing of the maxilla.

During feeding, the epaxial muscles show consistently large amplitude contractions, and electrical activity may be nearly continuous throughout the feeding sequence (Fig. 11:EP).

Mandibular depression may be initiated by one of several musculoskeletal couplings. The levator operculi is the first muscle to contract during feeding (Fig. 11:LOP) (with the occasional exception of hypaxial and epaxial muscles) and mediates lower jaw depression by rotating the operculum around its articulation with the hyomandibular and transmitting a caudodorsal force via the opercular series and the interoperculomandibular ligament to the lower jaw. This force is applied ventral to the quadratomandibular articulation and causes the tip of the mandible to swing ventrally (Fig. 10).

Movements of the hyoid may also contribute to mandibular depression by exerting a posterodorsal force on the retroarticular through the mandibulohyoid ligament (Fig. 10:l_2). This ligament stretches from the epihyal ventrally to the retroarticular and transmits a force produced by the sternohyoideus to the mandible. Since the contraction of the sternohyoideus consistently follows activity of the levator operculi, this coupling probably contributes to mandibular depression relatively late in the feeding sequence, shortly before maximum mouth opening is reached.

10.523 *Movements of the hyoid*

Depression of the hyoid during feeding is an important mechanism acting to increase the volume of the orobranchial chamber. Contraction of the sternohyoideus exerts a posteroventral force on the anterior of the hyoid arch (hypohyals) and exerts a moment around the interhyal-epihyal articulation and the hyomandibular-interhyal articulation causing the hyoid to pivot ventrally.

The kinetic relationships between the hyoid arch, interhyal, and suspensorium are extremely complex. Osse (1969, Fig. 22) hypothesized that the working line of the sternohyoideus in *Perca* was raised dorsally during the feeding sequence. In *Salvelinus*, however, the opposite occurs.

High-speed cineradiography of brook charr has allowed the first direct measurements of bone movements during feeding in fishes. This technique is particularly useful for measurements of hyoid movement since a direct measurement is not possible from light films. Anker *et al.* (1967) have measured bone movements during respiration in the stickleback, but the experimental subject was held in a clamp and filming was only at 42 frames sec^{-1}.

Activity in the sternohyoideus starts 5–10 msec after the levator operculi and epaxial muscles have begun to contract, but activity in the epaxial muscles, although elevating the neurocranium does not also elevate the working line of the sternohyoideus as hypothesized by Osse (1969). In fact, the working line of the sternohyoideus has dropped due to retraction and subsequent ventral rotation of the hyoid (Fig. 15:A, B, C). Elevation of the neurocranium does carry the interhyal anterodorsally to a slight degree but the effect of this motion on the hyoid arch is minimal because of the posterior location of the interhyal-hyomandibular articulation on the suspensorium and the highly mobile nature of this joint. By the time the neurocranium has begun to rotate dorsally on the anterior vertebrae of the vertebral column, the hyoid has been partially retracted and pivoted ventrally. The net effect, shown by the angle of the hyoid and the position of the marker just ventral to the sternohyoideus (Fig. 15:B) is that the working line of the sternohyoideus is depressed ventrally and is never raised dorsally even early in the strike.

The force generated by the sternohyoideus during contraction may be resolved into two components acting at right angles to each other. One component, initially the smaller of the two, is directed ventrally through the hypohyals and acts to depress the hyoid ventrally while the second component is directed posteriorly.

The effect of this component is to retract the hyoid posteriorly during the first half of the feeding sequence (Fig. 15: frames 1, 3, 6). Thus in addition to being carried dorsally by the neurocranium and pivoted ventrally by the ventral component of the sternohyoideus, the hyoid arch is also retracted.

Retraction and elevation of the epihyal has important consequences for mandibular depression. As noted earlier, depression of the lower jaw may be due to one or more of several couplings. One of these, the sternohyoideus-hyoid-mandible coupling, can only be activated by a caudodorsal movement of the hyoid. The mandibulohyoid ligament, originating dorsally on the epihyal will not transmit any force to the lower jaw as a result of hyoid depression alone. Retraction and dorsal movement of the epihyal are essential for the creation of tension in the mandibulohyoid ligament and the transmission of a caudodorsal force to the retroarticular process of the lower jaw.

The mechanical dependence of the sternohyoideus-hyoid-mandible coupling on dorsal and caudal movements of the hyoid suggests an important functional role of the interhyal bone. Hyoid retraction and elevation would not be possible independently of suspensorial movements if the epihyal articulated directly with the hyomandibular. In the first stages of a strike the suspensorium is carried anterodorsally and thus in a direction opposite to that needed for activation of the sternohyoideus-hyoid-mandible coupling. The interhyal thus permits movement of the hyoid in the opposite direction from that of the suspensorium during the early stages of the feeding sequence.

This analysis predicts that the interhyal will swing posteriorly during the first 50 msec of feeding and only later swing anteriorly as the hyoid moves ventrally or as the geniohyoideus protracts the hyoid.

Maximum ventral movement of the hyoid occurs 5–10 msec after maximum mouth opening has been achieved and corresponds well with sternohyoideus activity (Fig. 11:SH; 14). Hyoid depression is never synchronized with mouth opening and always reaches a maximum after the jaws have begun to close.

10.524 *Versatility in the cleithrum-hyoid-mandible coupling*

Elshoud-Oldenhave & Osse (1976) in *Gymnocephalus* and Lauder (1979) in *Hoplias* have suggested that a musculoskeletal coupling between the cleithrum, hyoid, and mandible mediated by the sternohyoideus, hypaxial muscles, and geniohyoideus can either adduct or abduct the mandible depending on the relative positions of the mechanical units. The hypothesized versatility of this coupling is due to a shift in the working line of the sternohyoideus and geniohyoideus muscles from below the quadratomandibular articulation during the middle of a strike to a position above the quadratomandibular articulation when the lower jaw is adducted at the end of the strike.

In *Salvelinus fontinalis*, such versatility in this coupling is highly unlikely, since the working line of the sternohyoideus never rises above the quadratomandibular joint. X-ray cinematography (Fig. 15) reveals that the hyoid remains depressed well after the jaws have closed (Fig. 14) and even in the initial rest position does not allow the working line of muscle action to pass dorsal to the jaw joint.

10.525 *Movement of the opercular series*

The measurement of opercular series movement (Fig. 11:LOP; 14) is quite complex since high-speed films allow only a two-dimensional analysis while the actual motions take place in three dimensions. The two main motions of the opercular series are levation (dorsal rotation), and dilation (abduction).

Levation of the opercular series occurs in the first 15–20 msec of the feeding sequence. The consequence of levator operculi contraction is a rotation of the operculum around its articulation with the hyomandibular. In brook charr, the muscle fibers of the levator operculi run posteroventrally from the neurocranium to the inner anterodorsal margin of the operculum (Fig. 4). As a consequence, the operculum is rotated by contraction of the levator operculi and the ventral margin moves posteriorly carrying with it the subopercular and interopercular. The posterior movement of the interoperculum is transmitted to the lower jaw by the interoperculomandibular ligament causing jaw depression.

Dilation of the opercular series (Fig. 11:DO;15) occurs relatively late in the feeding sequence. The maximum value of opercular dilation is reached 5 msec after hyoid depression reaches its maximum and is maintained for about 20 msec, slowly declining to its initial value long after the mouth has closed (Fig. 14). This presumably functions to permit the exit of water captured within the mouth during orobranchial expansion, and facilitates deglutition by allowing the continued flow of water to carry the prey towards the esophagus.

Electrical activity in the dilator operculi (Fig. 11:DO) generally precedes maximum dilation as measured from high-speed movies. Dilator activity begins nearly synchronously with contraction of the sternohyoideus and levator arcus palatini and may overlap the onset of activity in the adductor mandibulae.

The termination of dilator contraction is much more variable than the start; the first electrical activity in the dilator operculi consistently occurring 5–10 msec after the start of levator operculi activity, while the duration of activity depends on the rapidity of the strike and the size of the prey.

10.526 *Movements of the suspensorium*

Abduction of the suspensorium contributes greatly to the expansion of the orobranchial chamber. Anteroposterior movement of the suspensorium is limited and thus lateral movement is restricted to an axis formed by the joint between the neurocranium and hyomandibular posteriorly and the palatine and neurocranium anteriorly. Lateral movement of the suspensorium is temporally correlated with hyoid depression, the levator arcus palatini firing nearly synchronously with the sternohyoideus (Fig. 11:SH, LAP).

Elevation of the neurocranium during the first 15 msec after the mouth begins to open carries the suspensorium anterodorsally. This results in the quadratomandibular articulation and the suspensorial articulation of the interhyal also being carried anterodorsally and facilitates depression of the lower jaw by increasing the mechanical advantage of the ventral head couplings.

Elevation of the neurocranium and depression of the lower jaw begin the feeding sequence, increasing the gape and initiating water flow into the mouth. This event is followed by a steady increase in hyoid depression and suspensorial abduction which reach their maximum excursion 5–10 msec after peak gape. Opercular dilation reaches a maximum value 10 msec after maximum hyoid depression (Fig. 14). The peak values of each of the major movements contributing to orobranchial expansion thus occur sequentially in a consistent anteroposterior direction and may function to move the low pressure center in the buccal cavity posteriorly. Nyberg (1971) has noted this same phenomenon in the bass (*Micropterus*).

10.53 *Movements of the pectoral girdle*

The pectoral girdle has been generally ignored in studies of feeding in teleost fishes. Tchernavin (1953) has discussed the pectoral girdle and its contribution to the feeding mechanism of *Salmo salar* and *Chauliodus sloani*, but his analysis was based exclusively on the manipulation of preserved specimens. Similarly, Anker (1974) has suggested possible pectoral girdle movements in *Gasterosteus* and Osse (1969) has considered certain movements of the pectoral girdle of the perch.

High-speed X-ray cinematography of feeding in *Salvinus fontinalis* has allowed direct measurements of the pectoral girdle during feeding (Fig. 2, 15, 16). In general, the pectoral girdle moves considerably less than previous authors have predicted, and, surprisingly, the motion at the beginning of the strike is the opposite of published predictions.

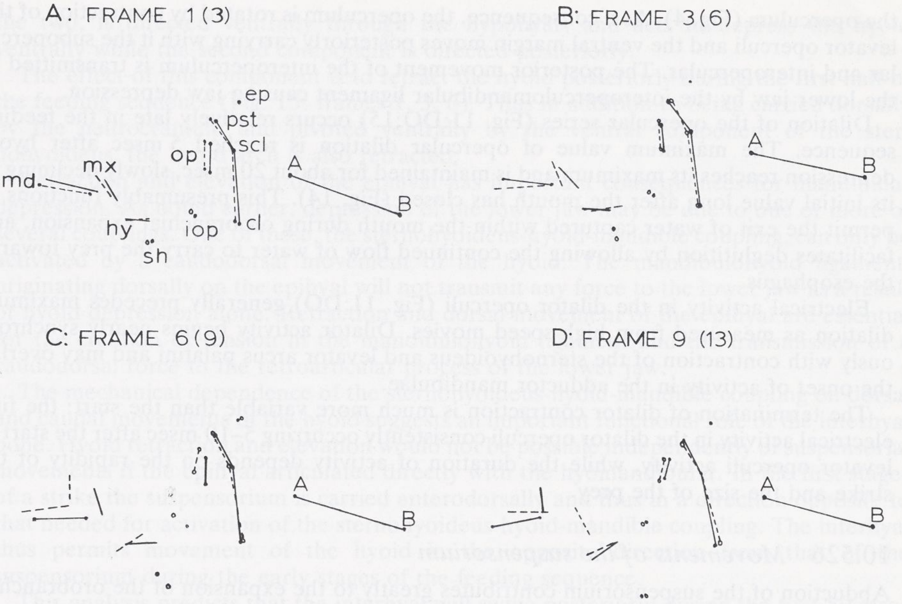

Fig. 15. Movement of the head during feeding in *Salvelinus fontinalis* as determined by high-speed (200 frames $\sec^{-1}$) cineradiography. The lines and the points represent the position of wires and screws implanted in the bones of the head (see Fig. 2). Each diagram shows the earlier position of the bones as solid lines and points, and the position at the later time (the frame number in parenthesis) as dotted lines or open circles. Note retraction of the hyoid between frames 3 and 6, hyoid depression between frames 6 and 9, and the motion of the pectoral girdle. Time between successive frames is 5 msec. Abbreviations: A–B, a line representing the vertebral axis; cl, a screw located in the cleithrum; ep, a lead marker located just dorsal to the epaxial muscle mass; hy, a wire located medially along the ceratohyal; iop, a screw located in the interopercular bone; md, the line formed by the two screws located in the lower jaw; mx, a wire located subcutaneously just lateral to the maxillary bone; op, a line between two screws in the opercular bone; pst, a screw in the post-temporal bone; scl, a screw in the supracleithrum; sh, a lead marker located just ventral to the sternohyoideus muscle mass.

The pectoral girdle is not a single mechanical unit, and since each of the three elements composing the pectoral girdle may exhibit movements at least partially independent of the other two units, the forces potentially influencing the motion of each of the three pectoral girdle bones will first be considered before the *in vivo* motions and patterns of muscle activity are described.

The post-temporal extends lateroventrally from its dorsal articulation with the neurocranium to the supracleithrum. As the neurocranium is elevated during feeding, the post-temporal may be carried dorsally and posteriorly since the point of post-temporal articulation with the neurocranium lies dorsal to the vertebral axis. The large protractor pectoralis (Fig. 7) will act to protract the post-temporal while the epaxial muscles will exert a posterior (retraction) force. Retraction is probably limited by Baudelot's ligament.

The supracleithrum is capable of some motion relative to the post-temporal, although a fairly stiff articulation exists ventrally with the cleithrum. The olbiquus superioris protracts the supracleithrum while the epaxial and dorsal hypaxial muscles exert a posterior force.

The cleithrum is subject to the greatest variety of possible influences. The sternohyoideus, obliquus superioris, and the pharyngocleithralis internus and externus (see

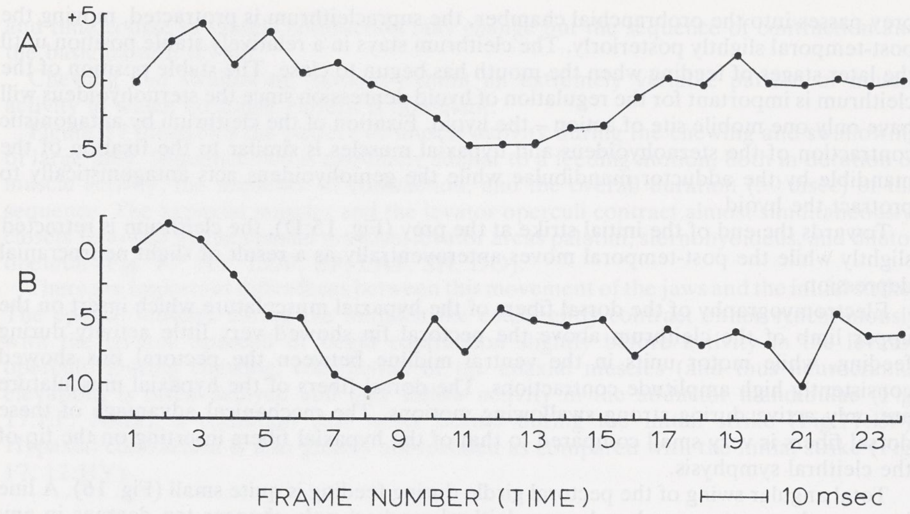

Fig. 16. Graphic representation of pectoral girdle movements during feeding based on measurements from high-speed (200 frames sec^{-1}) cineradiography. A: the angle between the supracleithral and cleithral markers and the vertebral column. B: the angle between the post-temporal and supracleithral markers and the vertebral column. Positive values indicate protraction, negative values indicate retraction.

Fig. 7) may all aid in protraction. The lateral and ventral hypaxial muscles may cause retraction during feeding. In addition, movements of the pectoral fin produce a constantly changing force on the cleithrum as the water pressure on the fin changes during feeding. The supracleithrum and cleithrum may also be lifted dorsally by elevation of the neurocranium.

The movements of the mechanical units in the pectoral girdle are thus the result of complex interactions between the four main muscles inserting on the girdle and their lever arms. Since all three mechanical units possess two mobile articulations, each unit will exhibit complex movements relative to the other units.

An integration of electromyographic evidence (Fig. 11:EP, SH, PP, HY) with cineradiographic data (Fig. 15, 16) reveals the following pattern of pectoral girdle movement during feeding.

In the early stages of the feeding sequence (Fig. 15:A), the entire pectoral girdle is raised dorsally due to the initial lifting of the neurocranium. Small anterodorsal movements of the two opercular points and the interopercular point corroborate this conclusion. At this stage the cleithrum is also slightly protracted (Fig. 11:PP, SH; Fig. 15).

Protraction of the cleithrum during the early stages of feeding is due to strong activity in the sternohyoideus and obliquus superioris which have just begun to contract. Nearly synchronous antagonistic contractions in the hypaxial musculature prevents large movements of the pectoral girdle and causes retraction of the cleithrum when sternohyoideus and obliquus superioris activity ceases (Fig. 15:D).

The discovery that protraction of the cleithrum occurs during the initial stages of feeding (the first 20 msec) is at complete variance with the suggestions of previous investigators. Both Tchernavin (1953) and Osse (1969) have illustrated the pectoral girdle as initially undergoing retraction as a result of hypaxial contraction. As shown here, the obliquus superioris and sternohyoideus cause protraction in spite of antagonistic activity in the epaxial and hypaxial muscles.

At a slightly later stage in the feeding sequence (Fig. 15:B), as the gape widens and the prey passes into the orobranchial chamber, the supracleithrum is protracted, moving the post-temporal slightly posteriorly. The cleithrum stays in a relatively stable position until the later stages of feeding when the mouth has begun to close. The stable position of the cleithrum is important for the regulation of hyoid depression since the sternohyoideus will have only one mobile site of action – the hyoid. Fixation of the cleithrum by antagonistic contraction of the sternohyoideus and hypaxial muscles is similar to the fixation of the mandible by the adductor mandibulae while the geniohyoideus acts antagonistically to protract the hyoid.

Towards the end of the initial strike at the prey (Fig. 15:D), the cleithrum is retracted slightly while the post-temporal moves anteroventrally as a result of slight neurocranial depression.

Electromyography of the dorsal fibers of the hypaxial musculature which insert on the upper limb of the cleithrum above the pectoral fin showed very little activity during feeding, while motor units in the ventral midline between the pectoral fins showed consistently high amplitude contractions. The dorsal fibers of the hypaxial musculature are only active during strong swallowing motions. The mechanical advantage of these dorsal fibers is very small compared to that of the hypaxial fibers inserting on the tip of the cleithral symphysis.

Total angular swing of the pectoral girdle during feeding is quite small (Fig. 16). A line between the posttemporal and supracleithral markers only changes ten degrees in any given direction while the cleithral and supracleithral markers swing through only a five degree angle relative to the vertebral column during both protraction and retraction.

These measured movements are quite small compared to those suggested on the basis of anatomical work only. Tchernavin (1953:11–12) states that in *Salmo salar*, "the main ventral part of the shoulder-girdle (. . .) plays an important role in the process of expansion of the pharyngo-oral cavity, and serves for the insertion of the ventro-lateral and ventral muscles, which pull back the shoulder-girdle and turn it downwards (. . .) The result of this movement (. . .) is that the posterior wall of the pharyngo-oral cavity formed by the cleithra and partially by the coracoids, moves backwards and downwards and the pharyngo-oral cavity becomes extended in length and depth." The rather small movements of the pectoral girdle in *Salvelinus* do not agree with Tchernavin's anatomical hypothesis and suggest that the movement of the pectoral girdle has very little to do with expanding the orobranchial cavity directly.

Osse (1969) has hypothesized that in the perch, the angle between the supracleithrum and the cleithrum remains fixed as the pectoral girdle is retracted and that the articulation between the post-temporal and the supracleithrum is the pivot for retraction of the cleithrum-supracleithrum complex. This situation is not the case in *Salvelinus* where the cleithrum may be retracted while the supracleithrum and post-temporal are simultaneously protracted (Fig. 15:D).

10.54 *Chewing and swallowing*

The previous analysis has been exclusively devoted to the initial prey capture and subsequent processing of the food has not been considered. Once the food has been captured, however, it must be manipulated into a position allowing deglutition. In many cases, especially with relatively small prey (*e.g.* Fig. 1), the initial expansion of the orobranchial chamber apparently serves to bring the prey posteriorly to the opening of the esophagus where it is easily swallowed. In these cases, very little EMG activity or bone movements are observed after the strike. Presumably the prey has been captured and swallowed in essentially one motion.

In many cases, however, the initial strike does not result in complete ingestion of the prey, either because it is too large or the prey is not positioned properly for deglutition. As the prey is positioned and prepared prior to swallowing, jaw movements may occur that are completely different from those seen during feeding. Generally, the initial strike at the prey by brook charr reveals a relatively consistent pattern in which the amplitude and time course of muscle contraction may change but the sequence of contraction and the basic pattern do not.

Chewing and swallowing motions exhibit an extremely variable pattern of muscle activity in which no single pattern is dominant.

Figure 17 illustrates the pattern of muscle activity during the chewing and swallowing of large prey. Sequence two is extremely similar to a feeding motion, both in duration of muscle activity, the sequence of contraction, and the overall duration (50 msec) of the sequence. The hypaxial muscles and the levator operculi contract almost simultaneously, closely followed by the epaxial muscles, levator arcus palatini, sternohyoideus, and dilator operculi (Fig. 17: HY, LOP, EP, LAP, SH, DO).

There are important differences between this movement of the jaws and the initial strike. The epaxial muscles during the initial strike consistently contract either synchronously with the levator operculi or begin contraction slightly before activity in the levator operculi. During chewing, contraction of the epaxial muscles (and thus neurocranial elevation) is often delayed and may follow activity in the adductor mandibulae (Fig. 17:EP, AM2), a condition that never occurs during the initial strike (Fig.11:EP). Hypaxial contraction is also greatly abbreviated as compared with the initial strike (Fig. 17, 12:HY).

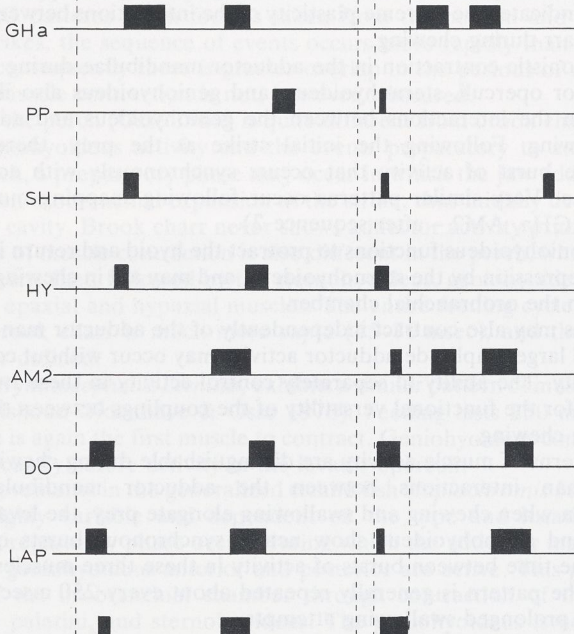

Fig. 17. Diagram of electromyographic recordings of muscle activity in nine cranial muscles during chewing and swallowing in *Salvelinus fontinalis*. The sequences labeled one and two represent patterns of activity respectively dissimilar and similar to EMG activity during feeding. Further discussion in the text. Muscles: AM2, second division of the adductor mandibulae; DO, dilator operculi; EP, epaxial muscles; GHa, anterior division of the geniohyoideus; HY, hypaxial muscles; LAP, levator arcus palatini; LOP, levator operculi; PP, protractor pectoralis; SH, sternohyoideus.

The rapid jaw movements just described are a common pattern during chewing and swallowing. The movements are generally similar to feeding and serve to draw the prey posteriorly and towards the esophagus.

In sharp contrast to these movements are other, less well defined, patterns of muscle activity (Fig. 17: sequence 1). Extreme variability in the sequence of muscle contraction is characteristic of these movements.

One musculoskeletal coupling possibly governing depression of the lower jaw is the cleithrum-hyoid-mandible coupling mediated by contraction of the sternohyoideus, geniohyoideus, and possibly also the hypaxial muscles. This coupling is not activated during feeding as noted earlier because the geniohyoideus shows no activity until after the jaws have closed. During chewing, however, this coupling is activated (Fig. 17: sequence 1:LOP, HY, SH, GHa). Activity in the levator operculi is slightly preceded by contraction of the epaxial and hypaxial musculature. A long period of levator operculi activity then occurs synchronously with contraction of both the sternohyoideus and geniohyoideus. This result conflicts with the conclusions of Ballintijn & Hughes (1966) who state that the geniohyoideus only protracts the hyoid.

The synchronous activity in the geniohyoideus, sternohyoideus, and levator operculi occurs in the absence of antagonistic activity by the adductor mandibulae, and thus it is highly unlikely that hyoid protraction is occurring. This simultaneous activity in the geniohyoideus and sternohyoideus only occurs during chewing and swallowing, never during feeding, and indicates the extreme plasticity of the interactions between the cranial muscles of brook charr during chewing.

The lack of antagonistic contraction in the adductor mandibulae during synchronous activity of the levator operculi, sternohyoideus, and geniohyoideus also illustrates the plasticity inherent in the interactions between the geniohyoideus and adductor mandibulae during chewing. Following the initial strike at the prey, there is often a characteristic double burst of activity that occurs synchronously with activity in the adductor mandibulae. Very similar patterns occur following snapping motions during swallowing (Fig. 17:GHa, AM2 – after sequence 2).

In this case, the geniohyoideus functions to protract the hyoid and return it to its initial position following depression by the sternohyoideus, and may aid in chewing by trapping the prey deep within the orobranchial chamber.

The geniohyoideus may also contract independently of the adductor mandibulae (Fig. 17: sequence 1) and large amplitude adductor activity may occur without corresponding geniohyoideus activity. The ability to separately control activity in these two muscles is entirely responsible for the functional versatility of the couplings between the hyoid and the mandible during chewing.

Several other patterns of muscle activity are distinguishable during chewing and show more regularity than interactions between the adductor mandibulae and the geniohyoideus. Often when chewing and swallowing elongate prey, the levator operculi, hypaxial muscles, and sternohyoideus show nearly synchronous bursts of activity at regular intervals. The time between bursts of activity in these three muscles varies from 200–300 msec but the pattern is generally repeated about every 250 msec for three or four seconds during prolonged swallowing attempts.

The obliquus superioris exhibits two main activity patterns during chewing and swallowing. One pattern is very similar to that seen during feeding (Fig. 17: PP-sequence 2). The other pattern is only observed in chewing and swallowing (Fig. 17: PP-sequence 1), and often alternates with the feeding pattern during prolonged swallowing motions. In the pattern occurring only during chewing, the obliquus superioris contracts almost in isolation, closely following activity in the dilator operculi and the hypaxial muscles. This relatively isolated contraction of the obliquus superioris may function to return the pectoral girdle to its initial position following retraction by the hypaxial muscles.

Osse (1969) in his study of the perch, noted a significant difference between activity in the two divisions of the geniohyoideus muscle. In brook charr, very little difference has been observed between contraction of the anterior and posterior divisions of the geniohyoideus.

10.6 **Discussion**

10.61 *The pattern of jaw movement in teleost fishes*

Throughout the course of actinopterygian evolution, the adaptive radiation in jaw morphology has been the main defining characteristic of the major levels of adaptation. The diversification of actinopterygians has been accompanied by an increasing complexity of the jaw apparatus with a concomitant increase in the mechanical independence of jaw elements.

In spite of the diversity and importance of the feeding mechanism, little is understood of variations in the basic patterns of jaw mechanics and feeding within the Teleostei. It is particularly important to compare the pattern of jaw movement in generalized primitive predators with that seen in generalized acanthopterygian fishes in order to establish how new functions are integrated into the existing feeding mechanism. The analysis of how a new complex feature is integrated into an existing character complex will provide a clearer understanding of the diversity of teleostean jaw morphology.

The pattern of muscle activity during feeding in brook charr is relatively consistent from one feeding sequence to the next, and the start of mouth opening is easily defined by the large amplitude contractions of the levator operculi, generally synchronous with high activity of the hypaxial and epaxial muscles. A consistent difference has been found between EMG patterns when food is taken from the bottom and from mid-water. In mid-water strikes, the sequence of events occurs more rapidly than in feeding from the bottom and consequently there is greater overlap in the periods of muscle activity. The sequence of muscle contraction is not, however, obscured.

Feeding in the perch (Osse 1969) is quite different from brook charr, particularly with regard to geniohyoideus activity and the events preparatory to and during the initial strike. In perch, a preparatory phase may occur in which the jaw adductors are activated prior to sudden orobranchial expansion at the strike, thus initially decreasing the volume of the buccal cavity. Brook charr never shows adductor activity prior to mouth opening. The sequence of muscle contraction is also different in the perch, where the levator arcus palatini contracts first, followed by the sternohyoideus, geniohyoideus, levator operculi, and then the epaxial and hypaxial muscles. The entire feeding cycle occupies 230 msec. Feeding in brook charr is much more rapid (45–70 msec), and the pattern of muscle activity better defined.

The ruffe, *Gymnocephalus cernuus,* exhibits a similar pattern of muscle activity to that of the perch (Elshoud-Oldenhave & Osse 1976). Feeding lasts 250 msec and the levator arcus palatini is again the first muscle to contract. Geniohyoideus contraction in the ruffe begins significantly before activity in the levator operculi.

Feeding movements in the generalized cichlid fish *Haplochromis burtoni* (Liem & Osse 1975) are highly variable and dependent on the type and location of the prey. A pronounced preparatory phase occurs during which the adductor mandibulae (part two) and both the geniohyoideus anterior and posterior are active. This phase is followed by expansion of the orobranchial chamber through contraction of the levator operculi, levator arcus palatini, and sternohyoideus. The geniohyoideus is not active during the initial phases of orobranchial expansion.

The main difference between the pattern of muscle activity recorded for brook charr and the data presented on percoids and cichlids lie in the preparation for the strike and the initial mouth opening. The brook charr is not primarily a suction feeder, although some suction can be created to draw prey off the bottom, and the EMG pattern reflects this. In *Haplochromis* and *Perca* the levator arcus palatini is strongly active before the levator operculi and the sternohyoideus contract to open the mouth, while in *Salvelinus*, the levator arcus palatini always follows the levator operculi. Early contraction of the levator arcus palatini in percoids may function to create a negative pressure in the buccal cavity prior to mouth opening and decrease the delay between the time the jaws open and the start of water flow into the mouth.

The presence of a preparatory phase and early levator arcus palatini activity in *Perca*, *Gymnocephalus*, and *Haplochromis* is related to the suction feeding mechanism. An equally striking difference between these fishes and *Salvelinus* is, however, not so easily explained. In the charr the geniohyoideus is never active during the strike (Fig. 11:GH) and only contracts during chewing and swallowing. This is in sharp contrast to the situation in *Perca* (Osse 1969, Fig. 20) and *Gymnocephalus* (Elshoud-Oldenhave & Osse 1975, Fig. 12) where activity of the geniohyoideus actually precedes contraction of the levator operculi. Clearly a fundamental difference in jaw opening couplings exists between charr and percoid fishes.

The role of the geniohyoideus in feeding is further complicated by our discovery that the cleithrum-hyoid-mandible coupling, not active during feeding, is active during chewing and swallowing in charr (Fig. 17). The activation of this musculoskeletal coupling depends not only upon activity of the geniohyoideus, however, but also upon the condition of antagonistic muscles. In *Haplochromis burtoni* (Liem & Osse 1975, Fig. 8), the preparatory phase exhibits antagonistic contraction of the adductor mandibulae (part two) and the geniohyoideus, while 200 msec later, during the second burst of activity, there is no antagonistic adductor contraction.

10.62 *Feeding mechanics and the evolution of the actinopterygian jaw*

One of the most important aspects of jaw evolution in actinopterygians is the increasing mechanical independence of jaw opening couplings. Not only have multiple functional solutions arisen to the single problem of opening the mouth, but these multiple solutions coexist and are capable of acting synergisticly to increase the efficiency of lower jaw depression, or acting independently to regulate events involving the timing of suction during feeding. The process through which functional solutions to mouth opening functions has been achieved is of paramount significance for an understanding of the mechanisms underlying the actinopterygian adaptive radiation.

The differentiation of the interopercular bone at the halecostome level allowed two independent musculoskeletal couplings to control lower jaw depression: the levator operculi-opercular series-mandible coupling and the cleithrum-hyoid-mandible coupling. Palaeoniscoid fishes were constrained to use only the ventral head muscles, perhaps in conjunction with the hypaxial muscles to control lower jaw depression (Schaeffer & Rosen 1961). The differentiation of the interopercular released the functional constraints upon the ventral head couplings and allowed them to undertake new functions (Lauder 1979) such as the timing of hyoid depression during the feeding sequence.

The role of the hyoid during feeding in the halecostome and paleoniscoid feeding mechanism must be reevaluated in light of the functional relationships of the hyoid discovered in charr. In particular, the important role of the interhyal bone must be considered in the evolution of the actinopterygian jaw.

The interhyal has at least two main functions in the feeding mechanism of fishes. First, it allows the hyoid to move in a dorsoventral plane with greater amplitude than otherwise possible due to the added link between the hyoid and the suspensorium. This increases the amount of orobranchial expansion both by reducing the initial buccal volume (through greater dorsal hyoid movement) and by increasing the ventral swing of the hyoid during depression. Secondly, the interhyal allows a posterodorsal movement of the hyoid (retraction) during feeding when the suspensorium is moving anterodorsally.

As ligamentous connections developed between the epihyal and the uppermost branchiostegal (as in *Amia*, Allis 1897) and between the epihyal and interopercular (as in teleosts and *Amia*), the posterodorsal hyoid movement would have been transferred to the interopercular and hence to the lower jaw causing it to rotate ventrally around the quadratomandibular articulation. Thus, the posterodorsal movements of the hyoid would activate another coupling mediating lower jaw depression; the sternohyoideus-hyoid-interopercular-mandible coupling. This coupling may have been of considerable importance in the early developmental stages of a true interopercular bone since an expanded upper branchiostegal ray (*e.g. Amia*) would have served equally well to transmit the posterior hyoid movement to the lower jaw.

The first occurrence of this coupling in the fossil record is difficult to establish due to the small size of the interhyal bone and the lack of attention it is given in the literature. The interhyal is unknown in chondrosteans (Schaeffer 1969, Lehman 1966) and the genus *Ospia*, a parasemiontid fish of the Lower Triassic, apparently represents the earliest record of an interhyal with a comparable morphology to the interhyal of teleosts (Lehman 1966). A more careful examination of earlier fossils may reveal a similar interhyal in all halecostome fishes. The interhyal bone is an important adaptation for suction feeding since it increases the mechanical independence of musculoskeletal couplings and allows greater expansion of the orobranchial chamber.

The mandibulohyoid ligament, present in charr and many other teleosts (see Verraes 1977 for a review), *Lepisosteus* (Wiley 1976), and *Amia* (Allis 1897) provides a direct connection between the mandible and hyoid. In charr, this allows yet another coupling, the sternohyoideus-hyoid-mandible coupling, to aid in depression of the jaw. Verraes (1977) has discussed the role of this ligament in respiration and feeding in rainbow trout eleutheroembryos and alevins. In *Salmo* the mandibulohyoid ligament develops before the interoperculomandibular ligament and controls respiration and feeding functions in the eleutheroembryos and alevins.

The exact role of the mandibulohyoid ligament in the evolution of the actinopterygian jaw is unclear. This ligament may have played an important role in depression of the lower jaw in paleoniscoid fishes where a direct connection between the hyoid and the mandible would have greatly facilitated lower jaw depression by activation of the sternohyoideus-hyoid-mandible coupling. Alternatively, the mandibulohyoid ligament may be a primitive character for neopterygian fishes (having been lost in higher teleosts). The sternohyoideus muscle would then have been the prime mediator of lower jaw depression in early neopterygians.

Acknowledgements

Many people have greatly aided in the preparation of this manuscript. Special thanks go to Michael Buckley, Kathie Cunningham, Karsten Hartel, David Kraus, Bob Schoknecht, and Jim Wallace. Sara Fink and Joshua B. Clark Jr. drew the anatomical figures, and Bill Fink and Wim Weijs offered valuable criticisms of the manuscript.

Vic Segarich of the Massachusetts State Hatchery in North Attleboro kindly provided specimens of *Salvelinus fontinalis* and Jim Morrow supplied specimens of *S. malma* and *S. alpinus*.

This research was supported by an NIH Predoctoral Fellowship (5T32 GMO7117–03) to George Lauder and NSF DEB76–04386 to Karel Liem.

References cited

Alexander, R. McN. 1967a. The functions and mechanisms of the protrusible jaws of some acanthopterygian fish. J. Zool., Lond. 151: 43–64.

Alexander, R. McN. 1967b. Mechanisms of the jaws of some atheriniform fish. J. Zool., Lond. 151: 233–255.

Alexander, R. McN. 1969. Mechanics of the feeding action of a cyprinid fish. J. Zool., Lond. 159: 1–15.

Alexander, R. McN. 1970. Mechanics of the feeding action of various teleost fishes. J. Zool., Lond. 162: 145–156.

Allis, E. P. 1897. The cranial muscles and cranial and first spinal nerves in *Amia calva*. J. Morph. 12: 487–808.

Anker, G. CH. 1974. Morphology and kinetics of the head of the stickleback, *Gasterosteus aculeatus*. Trans. Zool. Soc. Lond. 32: 311–416.

Anker, G. CH., J. Simons & P. Dullemeijer. 1967. An apparatus for direct x-ray cinematography exemplified by analysis of some respiratory movements in *Gasterosteus aculeatus*. Experientia 23: 74–77.

Ballintijn, C. & G. M. Hughes. 1965. The muscular basis of the respiratory pumps in the trout. J. exp. Biol. 43: 349–362.

Basmajian, J. V. & G. A. Stecko. 1962. A new bipolar indwelling electrode for electromyography. J. Appl. Physiol. 17: 849.

Dutta, H. M. 1968. Functional morphology of the head of *Anabas testudineus* (Bloch). Ph.D. Thesis, Univ. Leiden. 146 pp.

Dutta, H. M. 1975. The suspensorium of *Ctenopoma acutirostre*: a comparative functional analysis with *Anabas testudineus*. J. Morph. 146: 457–478.

Elshoud-Oldenhave, M. J. W. & J. W. M. Osse. 1976. Functional morphology of the feeding system in the ruff – *Gymnocephalus cernua* (L. 1758) – (Teleostei, Percidae). J. Morph. 150: 399–422.

Gans, C. 1969. Functional components versus mechanical units in descriptive morphology. J. Morph. 128: 365–368.

Greene, C. W. & C. H. Greene. 1913. The skeletal musculature of the king salmon. Bull. Bureau Fisheries 33: 25–29.

Greenwood, P. H., D. E. Rosen, S. H. Weitzman & G. S. Myers. 1966. Phyletic studies of teleostean fishes with a provisional classification of living forms. Bull. Am. Mus. Nat. Hist. 131: 339–456.

Günther, K. & K. Deckert. 1953. Morphologisch-anatomische und vergleichendökologische Untersuchungen über die Leistungen des Viscerocranial-Apparates bei Tiefseefischen der Gattung *Cyclothone* (Teleostei, Isospondyli). Z. Morph. Ökol. Tiere. 42: 1–66.

Günther, K. & K. Deckert. 1955. Zweiter Versuch einer morphologisch-anatomischen Funktionsanalyse der Nahrungserwerbs-und Atmungsapparate von Tiefseefischen. Zool. Beitr. (n.ser.) 1:241–365.

Kampf, W. 1961. Vergleichende funktionsanalytische Untersuchungen an den Viscerocranien einiger rauberische lebender Knochenfishe. Zool. Beitr. (n.ser.) 6: 391–496.

Kirchhoff, H. 1958. Funktionell-anatomische Untersuchung des Visceralapparates von *Clupea harengus* L. Zool. Jb. Anat. 76: 461–540.

Lauder, G. V. 1979. Feeding mechanics in primitive teleosts and in the halecomorph fish *Amia calva*. J. Zool., Lond. 187.

Lehman, J.-P. 1966. Actinopterygii. pp. 1–242. In: J. Piveteau (ed.) Traite de Paleontologie, Vol. 4, part 3, Masson et Cie, Paris.

Liem, K. F. 1967. Functional morphology of the head of the anabantoid teleost fish, *Helostoma temmincki*. J. Morph. 121: 135–158.

Liem, K. F. 1970. Comparative functional anatomy of the Nandidae. Fieldiana, Zool. 56: 1–166.

Liem, K. F. 1973. Evolutionary strategies and morphological innovations: cichlid pharyngeal jaws. Syst. Zool. 22: 425–441.

Liem, K. F. & J. W. M. Osse. 1975. Biological versatility, evolution and food resource exploitation in African cichlid fishes. Amer. Zool. 15: 427–454.

Meijer, N. W. 1975. Cranial motor nerves innervating superficial respiratory muscles in carp (*Cyprinus carpio* L.). Netherlands J. Zool. 25: 103–113.

Nyberg, D. W. 1971. Prey capture in the largemouth bass. Am. Midl. Nat. 86: 128–144.

Osse, J. W. M. 1969. Functional morphology of the head of the perch (*Perca fluviatilis* L.): an electromyographic study. Neth. J. Zool. 19: 289–392.

Rosen, D. E. 1973. Interrelationships of higher euteleosteans. pp. 387–513. In: P. H. Greenwood, R. S. Miles & C. Pattersson (ed.) Interrelationships of fishes, Academic Press, London.

Schaeffer, B. 1969. The origin and basic radiation of the Osteichthyes. pp. 207–222. In: T. Orvig (ed.) Current problems in lower vertebrate phylogeny, Almquist and Wiskell, Stockholm.

Schaeffer, B. & D. E. Rosen. 1961. Major adaptive levels in the evolution of the actinopterygian feeding mechanism. Amer. Zool. 1: 187–204.

Tchernavin, V. V. 1948. On the mechanical working of the head of bony fishes. Proc. Zool. Soc. Lond. 118: 129–143.

Tchernavin, V. V. 1953. The feeding mechanisms of a deep sea fish *Chauliodus sloani* Schneider. British Museum (Nat. Hist.), London. 99 pp.

Van Dobben, W. H. 1935. Über den Kiefermechanismus der Knochenfische. Arch. Neerl. Zool. 2: 1–72.

Verraes, W. 1977. Postembryonic ontogeny and functional anatomy of the ligamentum mandibulo-hyoideum and the ligamentum interoperculo-mandibulare, with notes on the opercular bones and some other cranial elements in *Salmo gairdneri* Richardson 1836 (Teleostei: Salmonidae). J. Morph. 151: 111–120.

Vetter, B. 1878. Untersuchungen zur vergleichende Anatomie der Kiemen-und Kiefermuskulatur der Fische. II. Jenaische Zeitschrift für Naturwissenschaft 12: 431–550.

Vrba, E. S. 1968. Contributions to the functional morphology of fishes, part V. The feeding mechanism of *Elops saurus* Linnaeus. Zoologica Africana 3: 211–236.

Wiley, E. O. 1976. The phylogeny and biogeography of fossil and recent gars (Actinopterygii: Lepisosteidae). Univ. Kansas Mus. Nat. Hist. Misc. Pub. 64: 1–111.

Winterbottom, R. 1974. A descriptive synonymy of the striated muscles of the teleostei. Proc. Acad. Nat. Sci. Phil. 125: 225–317.

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Library of Congress Cataloging in Publication Data
Main entry under title:
Charrs, salmonid fishes of the genus *Salvelinus*.
(Perspectives in vertebrate science; v. 1)
Bibliography
Includes index.
1. Salvelinus. I. Balon, Eugen K. II. Series.
QL638.S2C4 597'.55 79-23361

ISBN 90 6193 701 9

Cover design Max Velthuijs
Logos design Prof. Dr. Milan Klima

G. V. LAUDER
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Env. Biol. Fish. Vol. 7, No. 1, pp. 3–5, 1982

Mark Morton and his 'dolly varden – victim of piscatorial prejudice'

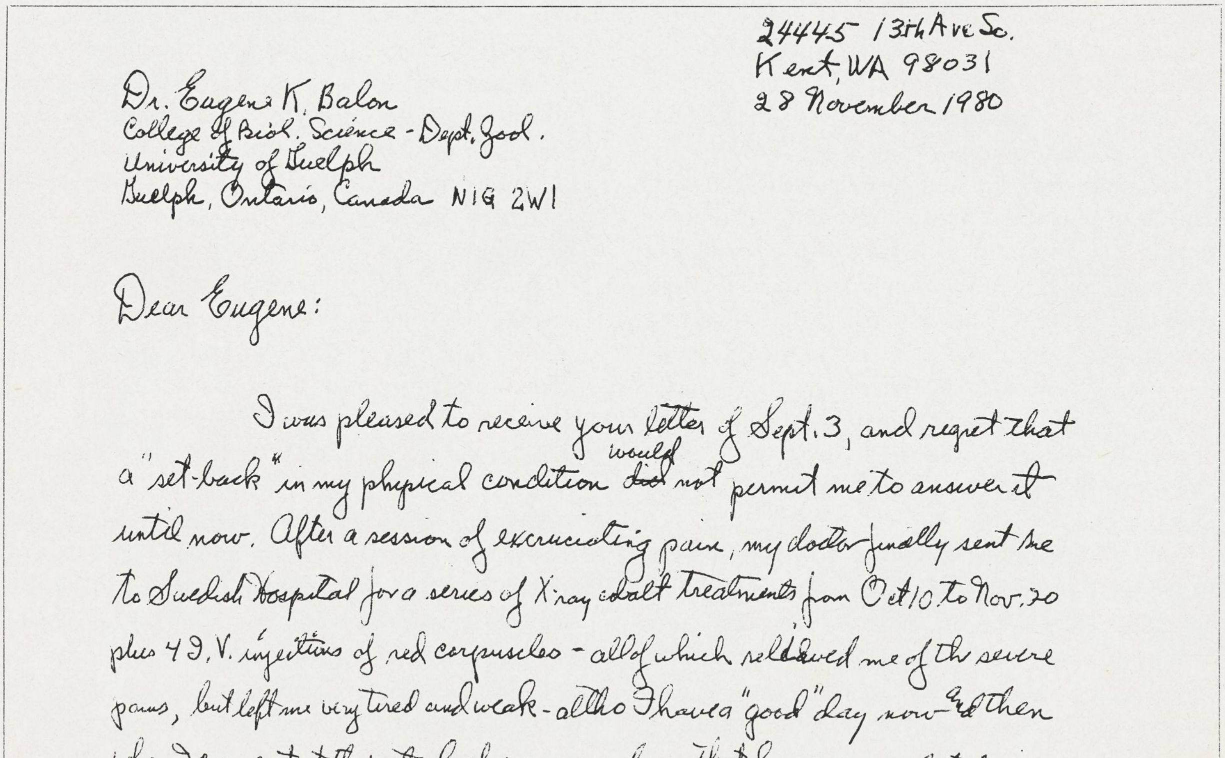
Eugene K. Balon

Department of Zoology, University of Guelph, Guelph, Ontario N1G 2W1, Canada

This is an obituary in which I wish William Markham Morton (24.11.1905–11.2.1981) to tell his story himself. My intrusion is unjustified, but without some selection and editing this would exceed our ability to publish at all. It is with much sorrow that I present the last as well as the early writings of a man I never met but for years sympathetized with for his impossible quest to let people know a 'trivial' truth they did not want to hear; for in their offices or committees Mark's facts conflicted with decisions taken earlier.

While attending the ASZ meeting in Seattle at the end of December 1980 I spoke twice, for the first and last time, with Mark on the telephone and agreed to have, under the above title, his story told as an Invited Editorial in this Journal. In the last painful weeks left he just managed to have the outline written.

His last letter to me starts as follows:



24445 13th Ave So.
Kent, WA 98031
28 November 1980

Dr. Eugene K. Balon
College of Biol. Science - Dept. Zool.
University of Guelph
Guelph, Ontario, Canada N1G 2W1

Dear Eugene:

I was pleased to receive your letter of Sept. 3, and regret that a "set-back" in my physical condition ~~did~~ would not permit me to answer it until now. After a session of excruciating pain, my doctor finally sent me to Swedish Hospital for a series of X-ray cobalt treatments from Oct 10 to Nov. 20 plus 4 I.V. injections of red corpuscles - all of which relieved me of the severe pains, but left me very tired and weak - altho I have a "good" day now and then when I can get at this stack of correspondence that has accumulated in the meantime. I get around with a cane and still have considerable chest pain.

0378-1909/82/0071-0003 $00.60

Several paragraphs later Mark's letter, as if he expected it to be the last one, goes on telling his story: 'You suggested an interest in a "guest editorial" on the general subject of "Dolly Varden – Victim of Piscatorial Prejudice" – a title I once used but which Jim Reardon would not accept for "The Dolly Varden is Innocent" (Alaska Magazine May '75 pp. 14–5; 62–3) which I wrote as a short popular style piece for quick consumption – xerox copy enclosed in case you have never seen it. This was a "boiled down" version of my main thesis entitled "Comparative Catches and Food Habits of Dolly Varden and Arctic Lake Charrs (*S. malma & S. alpinus*) at Karluk, Alaska, in 1939–1941". I revised this paper 8 times from 1945 to 1964 intending it for one of our (USF & WS) Scient. Invest.: Fisheries series but was refused. So after spending hundreds of hours and about $ 300 of my own funds I gave it up and filed it in my "soon-to-be-forgotten" file! Having done all the field work and writing in my spare-time I suppose it was ineligible for a government publication. I enclose one of my last revisions for your perusal (which I would like to have returned eventually) to give you some idea of the tremendous effort and general magnitude of the "basic data" for my hypothesis.[1] What is your proposed space limitation for such a story? Could you use colored photos or slides of the fish?

Or would you be more interested in the personal aspects of how this "albatros was hung around my neck"? It all began when, as a youth on a small farm in a small town in Wisconsin, I spent all my spare time chasing birds and butterflies, and collecting flowers, seeds, bird eggs et al. From the 8th grade on, I had a wonderful agriculture teacher who impressed upon me the personal satisfaction to be derived from greater productivity from my garden, chickens, bees, pigs etc. through improved feeding and breeding.

After graduation from Teacher's College in 1926 I tried for 12 years to find employment as a wildlife biologist. There were no vacancies nor jobs available in this field – so I spent those 12 years in the "glorified poverty" of a high school science teacher (coach & principal) – plus one of those years at Iowa University where I soon switched my major from Museum Techniques to zoological research.

I finally was offered a fishery biologist job in Seattle (at a $600 reduction from my H.S. Principal salary in 1938). I accepted it, and in the next 3 or 4 years got to realize what a foreigner I was to western fishery management. I was thrown into a mob of statisticians whose training at University of Washington or at Stanford had put the emphasis in fishery management on controlling the commercial fishermen and their catches as the best (and only) means of obtaining an optimum yield of halibut or salmon. A large part of their training also dealt with artificial propagation of salmonid species.

My first assignment as a permanent junior aquatic biologist was to assist Al DeLacy in 1939–41 in carrying on Tom Barnaby's marking an tagging experiments at Karluk Lake on Kodiak Island, Alaska. I had majored in parasitology under Dr. W. Riley at University of Minnesota during the summers of 1936 and 7, so it was only natural that when exposed to the first Dolly Varden trout I'd ever seen that I asked Al for permission to examine these beautiful fish for parasites before discarding after we took their measurements, weights, and checked for tags and/or marks. I was immediately impressed with the following observations: These downstream migrants were "sick" – very thin, and pale – and most of them had not been feeding for a long time; the only parasites were wads of cestodes & nematodes in stomach or pyloric caecal area. My big question to Al was: "How come we are killing thousands of these (to me) beautiful trout as a predator-control project when so few had any salmon migrants in their stomachs although millions were moving downstream alongside these trout? – in a 20 year program sponsored by the Territory of Alaska and approved by our Bureau of Fisheries?"

So when the spring run began to decline, we loaded up our gear in a skiff and worked our way up the 35 miles of Karluk River to Karluk Lake, where we continued our collection of specimens for marking and tag recoveries. I continued to examine the surplus fish for macro-parasites and was amazed at the differences in internal structure of the resident and anadromous trout. Our "lake" trout had pink tough swim or air bladders compared to the thin, transparent air sacs of the "ocean"

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[1] Edited version is published following this obituary.

trout. The former had pale or light brown livers compared to the reddish-purple colored livers of the latter. The lake types were loaded with parasites compared to lack of them in the ocean types. External differences were also very distinct.

So I asked Al (who had published several papers on systematics) how do you tell a "species" from a "race". He suggested beginning with meristic counts such as gill rakers, fin ray, scales etc. Well I had 6 specimens of each type on the table of our cabin on the morning of July 5, 1939 – and started out by counting gill-rakers. This initial observation indicated 22–27 gr. for the "lake" type and 17–21 for the "ocean" type. I'll never forget how surprised Al was at this difference – which needed *no* statistical analysis as there was no overlap! So I got all excited over this and put the emphasis on speciation & food studies and never really finished the parasitological work. I took a lot of "ribbing" from my contemporaries at Montlake Lab over the next few years I was there – especially over my thesis that the Dolly Varden Trout was 2 species of Charr; that the "ocean" type was an insignificant predator of salmon; and that the increasing numbers of sticklebacks would eventually replace young red salmon as the dominant inhabitants of Karluk Lake. The bounty on dolly varden was removed in 1942–3; the red salmon runs were a complete failure 12 years later due no doubt to the domination of sticklebacks! I broke up several staff conferences by demanding to know when our service was going to quit managing fishermen and start managing the fishes, habitat or environment!

One more thing – if I were young or healthy enough I'd surely enjoy attending that Arctic Charr International Symposium at Winnipeg[2] next May 4–7 to present my version of the ultimate general speciation of the "Arctic Charr Complex" or of Charrs of America in general – many features of which I do not find described in 'our' charr book.[3]

I have a letter from I.A. Chereshnev who says he and Dr. Glubokovsky plans to attend if they can get their reports in the program of the symposium. Dr. Chereshnev is at present my favorite "charrman". We see pretty much eye to eye in the true relationships of charrs. I'd like very much to meet him if he stops off in Seattle en route. Actually I may have moved on to the next world before that – but who knows about that?[4]

Hope you can make out my long-hand (can't climb the stairs to my "charr library" where my portable typewriter is located) or if so I can stay only a short time – so with apologies for this long maundering harangue... and for leaning so heavily on you to make an important decision for me.'

References cited

Morton, W.M. 1975. The Dolly Varden is innocent. Alaska magazine 41: 14–15, 62–63.

Morton, W.M. 1980. Goodbye Dolly. Fisheries 5: 17–21.

Silliman, R.P. 1981. William Markham (Mark) Morton. Fisheries 6: 32.

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[2] During the official part of the banquet the convener of this symposium Dr. Lionel Johnson asked me to receive in Mark's absence an Inuit carving given to him for his contributions to the knowledge of charrs. None of the ninety or so specialists assembled had been aware that Mark Morton died three months ago... The bulletin of AFS 'Fisheries' (Vol. 6, No. 2, p. 32), with the obituary, had not yet reached the subscribers.

[3] Charrs: Salmonid Fishes of the Genus *Salvelinus*. Perspectives in Vertebrate Science, Dr W. Junk Publishers, The Hague. 928 pp.

[4] No Soviet scientist in the end attended the Winnipeg Symposium.

Env. Biol. Fish. Vol. 7, No. 1, pp. 7–28, 1982

Comparative catches and food habits of dolly varden and arctic charrs, *Salvelinus malma* and *S. alpinus*, at Karluk, Alaska, in 1939–1941*

William Markham Morton

Formerly: Bureau of Sport Fisheries and Wildlife, Portland, Oregon, U.S.A.

Keywords:
Salmon predator, Bounties, Stomach contents, Fishing, Kodiak Island, Salmonid migration

Synopsis

For many years the seriousness of the predations of dolly varden (*Salvelinus malma*) upon the eggs, alevins and juveniles of Pacific salmons (*Oncorhynchus*) has been a controversial subject. Over $ 300,000 was spent in Western Alaska from 1920 to 1941 for bounties on dolly varden in the belief that they were serious salmon predators. The writer undertook this study because of an intense desire to evaluate the need and justification for such a bounty system. The incidental examination of stomach contents of charrs which were captured for tagging or for tag recovery purposes from Karluk Lake and Karluk River on Kodiak Island, Alaska, and from Shelikof Strait and Uyak Bay during the summer months of 1939, 1940 and 1941 presented an excellent opportunity to pursue such a project. Stomachs were collected and contents analyzed from 1,992 arctic charr (*Salvelinus alpinus*) and 2,565 dolly varden charr (*Salvelinus malma*), taken by beach seine, gill net, fyke net, hook and line and by weir trap from Karluk Lake; from 956 dolly varden taken by seine and weir trap from the Karluk River; and from 462 dolly varden taken by beach seine and commercial salmon traps in Uyak Bay. Among the more than 5,000 charr stomachs examined, only 42 were found to contain salmon smolts, parr or alevin. Examination of 500 stomachs taken from dolly varden charr captured in the lower Karluk River at the height of the red salmon (*Oncorhynchus nerka*) smolt migration in May of 1939 revealed very little evidence of predation on the smolts in fresh water. There was some evidence that this relationship may have changed after the migrating charr had become adjusted to salt water, although the examination of 460 stomachs of dolly varden captured in salt water revealed nothing particularly incriminating in its role as a salmon predator. The fact that the downstream migration of the dolly varden reached its peak before that of the red salmon smolts was considered significant. Examination of the 4,500 charr stomachs at Karluk Lake in the months from April through September led to the discovery that two distinct species of charrs were present, one, the dolly varden, primarily stream-inhabiting and anadromous, and the other, the arctic charr, primarily lake-inhabiting and nonanadromous. Although red salmon eggs constituted 32% of the total volume of food ingested by both species of charr at Karluk Lake, there was considerable evidence that they were consumed in salvage or scavenger feeding, and there was practically no evidence that they were consumed as a result of predatory feeding. Only five, or one-tenth of one percent, of the thousands of charr stomachs examined at Karluk Lake contained red salmon parr or alevin.

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* Published post mortem in shortened and slightly edited version. Reprint requests to the Editor.

Received 3.12.1980 *Accepted 1.6.1981*

A summary of the contrasts in the feeding and migratory habits and physical characteristics of *Salvelinus malma* and *Salvelinus alpinus* led to the conclusion that *alpinus* was a more serious potential salmon predator than *malma* at Karluk Lake. In view of the fact that *alpinus* was seldom reached by the predator-control program whereas *malma* was being systematically destroyed only because it was more easily captured due to its migratory tendencies, it was recommended that the predator control program be terminated in Karluk waters.

Introduction

This is the third of a series of papers on observations made on the dolly varden charr,[1] *Salvelinus malma* Walbaum (1792), commonly referred to in America as the Dolly Varden 'trout'; and the arctic charr, *Salvelinus alpinus* Linnaeus (1758), from the Karluk River system on Kodiak Island, Alaska. The first paper of this series dealt with the taxonomy of these fishes (DeLacy & Morton 1942). The second was a review of DeLacy's doctoral thesis (1943) dealing with their life histories. The purpose of this paper is to demonstrate some of the differences between these two species with respect to their distribution and food habits within the same watershed, and to show some of the ecological relationships between charrs and other species of fish in the Karluk system.

According to Cobb (1930, p. 454), 'One of the greatest salmon streams in the world is the Karluk River, and although its importance is much diminished now through long-continued and heavy fishing, it still produces annually a large pack of canned salmon, and has the distinction of having produced more salmon than any other river in Alaska.' The gradual decline of this famous red salmon run from 3,400,000 fish caught in 1889 to 5,000 caught in 1914 (Barnaby 1944, p. 239), brought demands from the industry for biological investigations by the U.S. Bureau of Fisheries. Initiation of such biological studies was delayed for several years because of World War I.

A similar decline in red salmon catches during the same period in the Bristol Bay Area stimulated Dennis Winn, U.S. Bureau of Fisheries agent in Alaska and a former hatchery superintendent, to organize and put into operation in 1920 a program of general predator control in the Bristol Bay area which was financed entirely by an association of Bristol Bay packers until 1926, at an average annual cost of about $17,000 (Winn 1920, 1921, 1922, 1923, 1925). In 1929 the territory of Alaska appropriated $40,000 and in 1931, $25,000 '...for cleaning salmon streams and for the destruction of predatory enemies of salmon, and declaring an emergency,...' according to Chapter 117 H.B. 121 Session Laws of the 1931 Legislature of the Territory of Alaska. Thereafter The Bristol Bay Packers' Association matched the territorial funds by raising $25,000 on each biennium until 1941. The Bureau of Fisheries approved all vouchers presented by collectors of 'trout' tails[2] (bounties ranged from 5 cents in 1920 to ½ cents each in the early 1930's), and the Association then paid checks on the approval of the Bureau. The packers assessed themselves every other year on the basis of their share of the pack the previous year to furnish their share of this fund. The Bureau of Fisheries cooperated further in the program by encouraging the destruction of dolly vardens whenever possible by its salmon-counting weir attendants, stream-guards and other employees. This program was finally dropped in 1942.

The resulting long-term investigation of the red salmon runs to the Karluk River, which was inaugurated by the Bureau of Fisheries in 1920 (and is continued today by the Bureau of Commercial Fisheries, the Fisheries Research Institute, and the State of Alaska), was expanded in 1935 by J.T. Barnaby to include a study of the role of Karluk 'trout' as salmon predators. In 1936 he made over 500 stomach examinations (Higgins 1938, pp. 32–

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[1] The writer cannot agree with the recently rising trend to fix 'char' as the correct spelling of this term. Considerable research into the subject has convinced him that, etymologically and historically, 'charr' is the more correct form of spelling, and he has so published (Morton 1955).

[2] Only tails were kept from fish over 15 cm long, usually salted or dried and strung on a wire. Fish smaller than 15 cm in length were submitted whole in a dried or salted condition for bounties.

33), and in 1937 inaugurated an extensive tagging program to study the movements, growth and stock size of the dolly varden. When Barnaby was transferred to Bristol Bay in 1938, his assistant, A.C. DeLacy, continued the trout program at Karluk until 1941 and presented a summary of the data collected in his doctoral thesis (DeLacy 1943). Early returns from this four-year tagging program indicated there were two distinct stocks of dolly varden in Karluk Lake (Higgins 1939, p. 39, 1940, p. 43).

In 1939, one of my first assignments was to assist DeLacy in the daily capture and destruction of several hundred large dolly varden as part of the general predator control program then in effect in Alaska (Fig. 1). This experience stimulated an intensive study of the stomach contents of these fish to ascertain their true relationship to the salmon of the Karluk River system. The primary motive for this food study was to try to determine the degree of predation on the red salmon eggs, alevins and juveniles by the charrs indigenous to the Karluk watershed.

Fig. 1. A skiffload of dolly varden captured and killed at the salmon-counting weir near the mouth of the Karluk River in May, 1939. Note the smolt-like appearance of these fish.

During the summers of 1939, 1940, and 1941 I examined almost 5,000 charr stomachs. In addition, meristic, morphometric and parasitological studies were made of over 300 specimens collected incidental to the tagging work. These studies established two facts: 1) that the two stocks of dolly varden 'trout' were two distinct species of 'charr', the true dolly varden (*Salvelinus malma*) and the arctic charr (*Salvelinus alpinus*), inhabiting the watershed (DeLacy & Morton 1942), and 2) that although these two species of charr displayed marked differences in distribution, anatomy, morphometry, ecology, and parasitology (Morton 1942), and food habits, there was a uniform lack of salmon alevins and juveniles in their diets.

Materials and methods

The Karluk watershed (see Fig. 2) is located in the northwestern section of the Kodiak Island, Alaska. Excellent physical, limnological and ecological descriptions of the area have been presented by Juday et al. (1932), Gilbert & Rich (1927), Bean (1891), and by Greenback & Nelson (1959).

The Karluk River system can be divided into three general habitat areas: Karluk Lake, Karluk River, and the marine area in Shelikof Strait and Uyak Bay. The Karluk Lake area consists of Karluk Lake, Thumb Lake, O'Malley Lake and their tributaries.

Karluk Lake, 19.2 km long by 3.2 km wide, is surrounded by mountains that rise steeply to a height of 762 m. It has a typical U-shaped basin indicative of its recent glacial origin. The maximum depth is 126 m, and the 9,728 surface acres of the lake are only about 107 m above sea level. The lake is characterized by a very limited littoral zone, the bottom usually falling away sharply from the shore which is composed, for the most part, of sharp, black slate-like shale rock with a few shallow beach areas of finely ground black shale. The lake usually freezes over in winter, and in summer the maximum surface temperature seldom reaches 15°C and

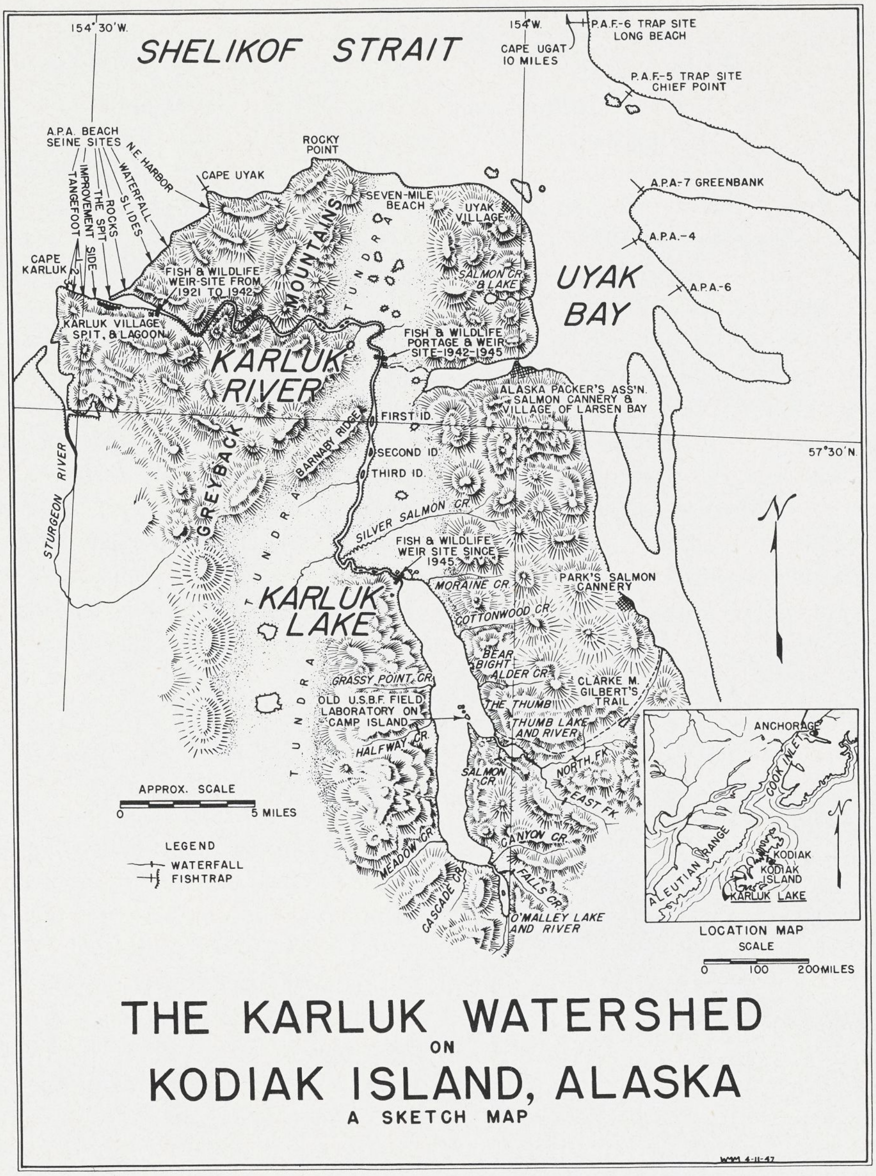

Fig. 2.

usually ranges between 10 and 14°C.

The Karluk River, about thirty miles long, has no obstructions to the passage of fish from Shelikof Strait to Karluk Lake. The only significant tributary to the Karluk River is Silver Salmon Creek which is about 4.6 m wide. Karluk River is estimated to have had an average flow of about 500 c.f.s. at the time of the study. The stream varies in width from 18 to 180 m before it reaches the 500 m wide estuary at its mouth.

Collection methods and catches made

Charrs used in this study were captured primarily for the purpose of tagging or for tag recoveries in the Karluk Lake area at the old salmon-counting weir near the mouth of the Karluk River from 1939 through 1941 and in the six commercial salmon traps and beach seines in Shelikof Straits and Uyak Bay from 1937 through 1941. Descriptions of the gear used and a summary of the catches made are presented to compare the results obtained by the various types of gear employed; to demonstrate the differences in seasonal distributions of *Salvelinus malma* and *Salvelinus alpinus* coinhabiting the same watershed; and to give some indication of their comparative abundance with other species taken.

At Karluk Lake

Charrs were captured in the streams entering Karluk Lake or off their mouths, by a small beach seine, a small weir trap in the Lower Thumb River, and by angling with hook and line. Charrs were taken from the lake by means of two gill nets, a rigid fyke net, and by angling with hook and line.

A beach seine (2 by 15 m) of 15 mm stretched-mesh webbing used at the mouths or the adjacent black shale-gravel beaches of streams emptying into Karluk Lake produced more fish with food in their stomachs than any other type of gear except hook and line. Because of its fine mesh, the gear could not be considered selective, yet only one juvenile charr was taken, along with very few smaller fish of other species. Juvenile fish apparently did not mix with adult charrs feeding off the mouths of streams, although they did mix in the streams and in the lake. Before the adult red salmon appeared off these stream mouths in June, most beachseine hauls made for charrs resulted in 'water hauls'.

After examining hundreds of specimens I decided to consider all charrs less than 20 centimeters in fork length as juveniles and all over this fork length as adults. Studies made on the dwarfed form of dolly varden found above high falls in streams tributary to Karluk Lake are not included in this paper. Some of these tiny charrs matured at 10 cm in length.

After July 1, when the spring runs of red salmon were schooled at the stream mouths, it proved such a difficult and time-consuming task to sort out the few hundred charrs from the hundreds of voilently active red salmon taken in these hauls, that the use of hook and line was resorted to for the capture of charrs, as the red salmon practically never took the hook. However, after the salmon had moved into the streams and started spawning, it was a simple matter to capture by seine-hauls large numbers of dolly varden and arctic charr as they lay in dense schools off the stream mouths where they fed on the drifting salmon eggs, various insect forms dislodged by the active spawners, and drifting particles of salmon flesh from the torn carcasses of red salmon partially eaten by the Kodiak bears. Most of the hauls were made at Halfway Creek.

A small counting and tagging weir or picket fence across the Lower Thumb River was screened to force upstream-moving fish into a trap, and this trap caught almost as many charrs as all the rest of the gear types combined. It was fished more than any other type of gear because 1) it was the most efficient, requiring very little attention in return for the daily catch of fish it made, and 2) the fish could be held alive until needed for tagging or tag recoveries which, of course, was the primary function of the installation. However, the gear was selective of smaller fish as the fence was open at each end to assure free passage for adult salmon upstream past the obstruction. As would be expected, over half of the stomachs examined were empty due to their confinement, and the area being sampled was not especially desirable from a food-study angle.

Fishing by hook and line was resorted to only when necessary to remove charrs desired for tagging or tag recoveries from large schools of red salmon concentrated at the stream mouths, or to capture the landlocked dwarfed form of dolly varden from mountain streams that flowed into the lake.

Good catches of arctic charr over 15 cm were usually made by the two experimental gill nets (each 38 m long, composed of five 7.5 m sections of 37, 50, 75 and 100 mm stretched cotton mesh) which were usually set in from 4.5 to 60 m of water, most frequently near Camp Island or off the mouth of Halfway Creek. On September 9, 1939, an arctic charr was taken in a set made in 10 m of water.

The fyke net used in Karluk Lake was an experimental trapnet modified somewhat from the standard design for this type of gear (Fig. 3). The Karluk net was designed with the original intention of fishing it at various depths in still water rather than in a stream; therefore, it was necessary to supply a rigid support for the net in order to keep it properly opened. This was achieved by building a frame around which the net was hung. The frame was 1.5 m^2 at one end and 1 m^2 at the other. Waterproof plywood strips were used in making the

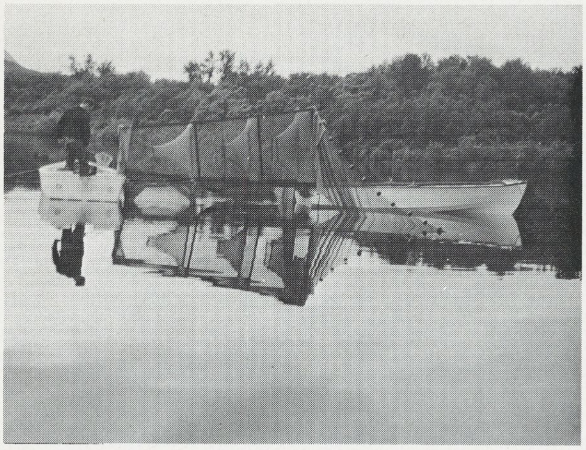

Fig. 3. Lifted fykenet in preparation for brailing.

frame, and all corners were reinforced with angle iron. Leads, 15 m in length, were attached to the large end of the frame, and when set they formed approximately a ninety-degree angle. Three funnels or throats served to lead the fish into the small end of the net. Twelve mm stretched-measure cotton netting was used throughout.

The fyke net was usually fished on the bottom in from 3 to 60 m of water. It was a cumbersome piece of gear that required about an hour to set or to raise and brail. It was raised by gently lifting the corks and slipping a flat-bottomed boat under the front lip, and then gradually raising the stern to a level with another boat with live-box attached; the bunt was untied and the fish brailed into a live-box.

Although charrs were taken in all sets, the largest catches were made in the 6 to 7.5 m depths around Camp Island. Fyke net catches from deep water were especially interesting. An August 20, 1941, the net, set in 60 m of water, caught 13 juvenile arctic charrs, 1 juvenile dolly varden, 4 sculpins and a black leech (*Erpobdella*). On September 10, 1941, in 25 m of water it captured 38 juvenile and 26 adult arctic charrs, 6 juvenile and 3 adult dolly varden, 2 juvenile red and 2 juvenile silver salmon, 12 three-spined sticklebacks, and 2 aleutian sculpins.

The fyke net was the most unselective piece of gear employed. It was the only device by which we could obtain, 1) a complete size series of juvenile arctic charrs and, 2) a rough cross-section of the fish stocks inhabiting the lake bottom area.

Marking experiments (DeLacy 1941) had established the fact that *Salvelinus alpinus* showed little tendency to move very far from the place they were marked or tagged, whereas there was a general exodus of adult *Salvelinus malma* from the lake during April and May to the sea from which they returned in July and August. Except for 8 steelhead taken in one beach-seine haul in April, all *Salmo gairdneri* taken were non-anadromous rainbow trout from the Lower Thumb River. Studies of scales of 3 to 5-year old fish captured showed no marine history.

By far the most common salmon at Karluk Lake was the red or sockeye salmon (*Oncorhynchus nerka*). Over 1,000,000 of these fish were allowed to escape the fishery and spawn in the lake in 1940. In that same year an overflow of a few thousand spawning pink or humpback salmon (*Oncorhynchus gorbuscha*) from the Karluk River found their way into tributaries of Karluk Lake. Practically none were observed at the lake in the 'off' cycle years of 1939 and 1941. The writer did not see over a half-dozen adult silver salmon (*Oncorhynchus kisutch*) during the three summers he spent at the lake as this species does not spawn in the tributaries until late in the fall. Several dwarfed adult red salmon resembling kokanee were recorded, and two dwarfed adult silver salmon were collected. The only non-salmonid species taken in the Karluk Lake area were the threespined stickleback (*Gasterosteus aculeatus*) and the Aleutian sculpin (*Cottus aleuticus*).

Every effort was made to avoid taken the adult red salmon in any of the gear used, and although every effort was made to try to capture juvenile red salmon with all available gear, such efforts were unsucessful. The only significant sample we ever collected at Karluk Lake was made in May of 1940 when 188 smolts were dipped from the Thumb river while a small school of these fish was observed moving downstream from Thumb Lake to Karluk Lake. We did not find these little fish in any significant numbers in our gear nor in the stomachs of predatory fish and birds we examined. On clear calm days the pelagic fish schools seen near the surface well out in the lake were observed at close range to be composed entirely of sticklebacks.

At Karluk River mouth

The gear used to capture charrs in the Karluk River was a combination of beach seine and weir trap employed at the original salmon-counting weir which had been installed by the Bureau of Fisheries in 1921, at the upper end of the brackish estuary or lagoon at the mouth of the Karluk River. This weir, similar in design to that described by O'Malley (1920) was essentially a 122-m-long picket fence reaching from bank to bank with pickets spaced at intervals of 3.5 cm (Fig. 4).

Bernaby and DeLacy had learned from their tagging experiments of 1937 and 1938 that the seaward migration of dolly varden at Karluk occurred in April and May, and that they returned from the sea to the river in large numbers in July and August. They also learned that, in order to make an effective barrier to these charrs, it was necessary to place 2 cm mesh chicken wire netting on the entire face of the weir. As these fish schooled up in front of the weir during the downstream migration in late April and May, they were captured by seining. In this work, advantage was taken of a shallow area near the middle of the river. On it a fence of wire netting was built perpendicular to and in front of the weir (Fig. 5). At the upstream end of the fence was placed a wire live-box fitted with a gate on the downstream side. A short wing of wire fencing was built out toward the area that was to be seined. With the gate to the pen open, a seine haul was started as shown in Figure 5. The upper end of the seine was brought downstream with the current and swept across the front of the weir and finally upstream along the wire fence, until the fish were all concentrated in the trap and the gate closed. As many as 1,800 dolly varden charrs were taken in one haul by this method.

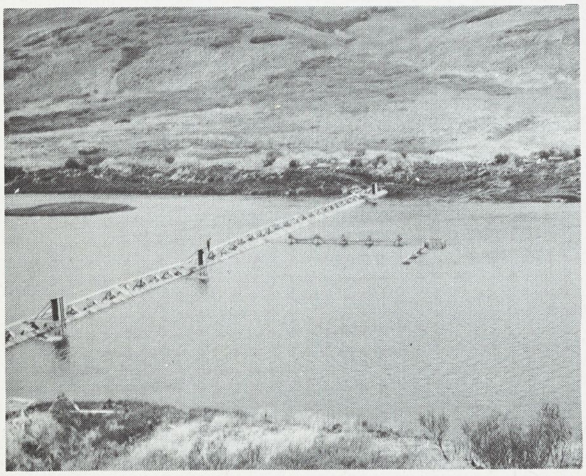

Fig. 4. The salmon-counting weir at the mouth of the Karluk River on May 28, 1941.

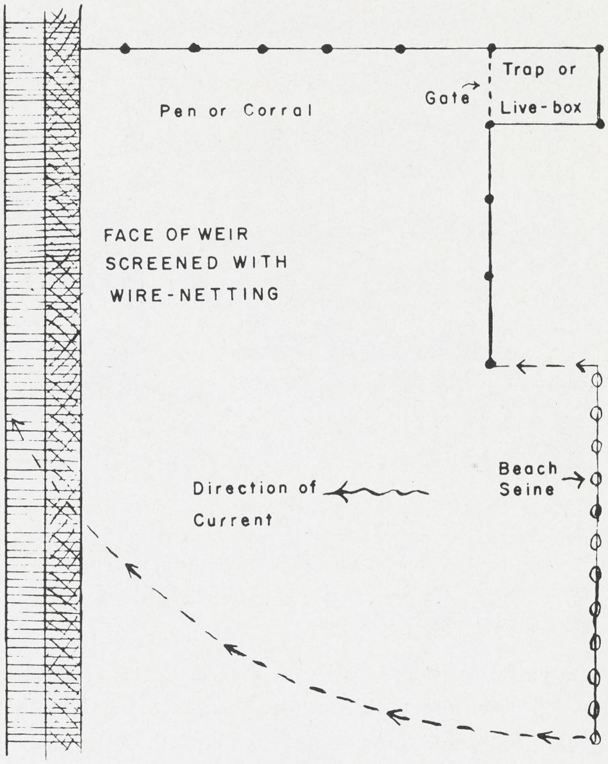

Fig. 5. A sketch of the method employed to capture downstream migrating dolly vardens at the Karluk weir.

Although some charrs, less than 15 cm in length, could pass through the wire mesh used, very few specimens less than 20 cm in length were even caught or observed at any time at the weir site. The seine method was considered to be one of the most non-selective types of sampling used. The charrs migrating downstream at this period were composed almost entirely of silvery smolt-like adult dolly vardens (Fig. 6). About a half dozen arctic charrs (*S. alpinus*), reddish in color and lacking the silvery tone (or guanine) were found among them each season. The latter had seen considered a color phase or race of dolly varden previous to 1940.

Sampling of the charrs returning from the sea was accomplished during July by the use of a weir

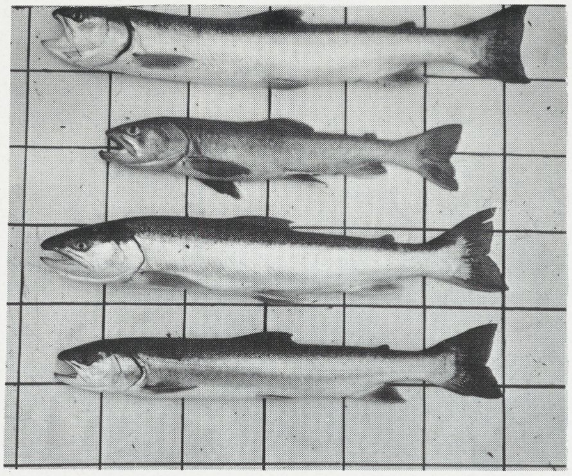

Fig. 6. Three seaward-migrating *Salvelinus malma* and one *Salvelinus alpinus* (second from the top) from the Karluk River salmon counting weir in May 1941. Note the typical smolt-like silver sides of the *malma*, its absence in the *alpinus* and the poor condition of both species.

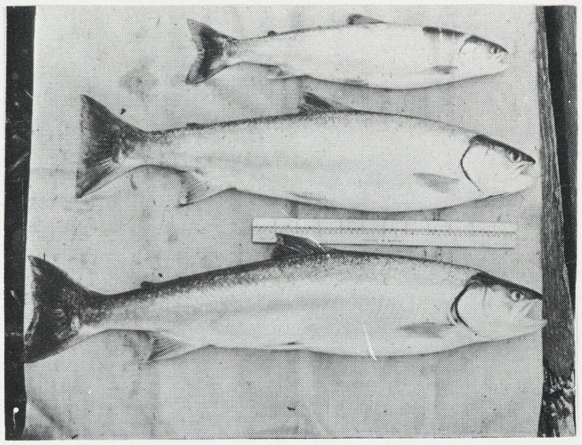

Fig. 7. Three *Salvelinus malma* from a commercial beach-seine haul for red salmon at the spit off the mouth of the Karluk River in Shelikof Straits in late June, 1941. Note the bright sides and excellent condition of the fish after spending some time at sea.

trap similar to the one used on the Lower Thumb River. Although this method was very effective (daily catches ranged from 1,000 to 5,000 dolly vardens), it yielded a decidedly selected sample of the charr population as fish over forty centimeters in length could not pass between the pickets, and therefore, all of the larger (and many of the smaller) fish passed the weir through the counting gates. In contrast to the poor condition of the smolt-like silver sided adults observed in the spring (Fig. 6) these upstream-moving dolly varden were fat and in all stages from slightly silvery (Fig. 7) to the typical general over-all dark green coloration with pale pink spots appearing on the side. Counts of upstream charr migrants at the peak of the summer run in July were made only in 1938 and 1939.

Table 1. Comparative commercial salmon-trap catches of salmon and charrs. No data available on *S. alpinus* in 1937 and 1938.

	Oncorhynchus					*Salvelinus*	
1937	*tshawytscha*	*nerka*	*gorbuscha*	*kisutch*	*keta*	*malma*	*alpinus*
June 24–29	109	9,935	88,128	0	673	630	–
July 8–9	17	5,343	33,210	104	1,205	714	–
July 15–20	43	16,163	147,946	1,111	2,574	2,127	–
July 24–29	0	1,401	137,053	277	3.021	2,450	–
Aug. 3–7	0	7,183	46,339	1,323	1,886	1,150	–
Aug. 9–13	8	11,332	123,907	2,193	2,299	462	–
Sept. 2–10	4	43,212	1,807	4.994	1,009	5	–
Total	181	94,569	578,390	10,002	12,667	7,538	–
1938							
June 29	14	1,663	46	0	581	2	–
July 7–13	273	1,780	1,322	15	12,922	1,623	–
Total	287	3,443	1,368	15	13,503	1,625	–
1939							
July 9–13	232	15,831	23,896	42	9,125	5,199	1

Among the thousands of dolly varden examined in July of 1939, only two arctic charr were found migrating upstream.

At sea

Thousands of dolly varden charrs were killed annually by the four types of salmon-fishing gear employed by the commercial fishery from Cape Karluk to Uyak Bay. Two of these types were of a mobile nature: 1) the purse-seine fishing vessels, and 2) the Alaska Packers Association 300-fathom-long, power-operated beach seines which fished near the mouth of the Karluk River. The other two types were of an immobile or stationary nature: 1) the local gill-netters who occupied the same sites year after year from Cape Uyak to Parks Cannery in Uyak Bay, and 2) the huge, pile-driven traps that extended out from the shore.

The salmon caught for commercial purposes by gillnets, purseseines, or beachseines in the Karluk area were pughed individually into cannery lighters or tenders standing by to haul the daily catches to nearby canneries. For this reason, very few other species of fish were ever found among these salmon when they arrived at the cannery.

The fish caught in the traps, on the other hand, were brailed into scows or lighters which were towed to the Alaska Packers Association cannery at Larsen Bay. At the cannery the fish were all sluiced from the scow into the elevator and sorted into bins, all species other than salmon and steelhead trout going to reduction. All deliveries to the cannery were examined carefully for marked red salmon and tagged dolly varden charr during 1937, 1938 and 1939 canning seasons. This cannery did not operate in 1940 and 1941. By combining the counts on the number of dolly varden examined from known trap-catches with the official trap catch report of salmon for the same trap-days, the scattered catch records were compiled in Table 1. These figures are presented here to show: 1) the relative abundance of these charrs with other salmonids at sea and, 2) that the charrs dropped off in abundance by September, reflecting their return to fresh-water to spawn. Only one arctic charr was found among the thousands of dolly varden examined from the sea in 1939.

Table 2. Volumetric displacement of countable stomach content items from Karluk charrs during summers of 1939, 1940, 1941.

	Number measured	Volume per item in cm^3	Number of organisms per 1 cm^3
Fishes			
Pink salmon 2.5 cm long	20	0.25	4.0
Silver salmon 5–8 cm	2	2.70	0.4
Silver salmon 8–10 cm	1	5.00	0.2
Red salmon eggs	1150	0.14	7.1
Red salmon egg shells	166	0.05	20.0
Sticklebacks less than 2.5 cm	229	0.04	25.0
Sticklebacks 2.5–5 cm	12	0.83	1.2
Sticklebacks 5–8 cm	8	2.80	0.4
Sticklebacks 8 cm or over	4	4.50	0.2
Sticklebacks skeletons	19	0.95	1.1
Stickleback eggs	924	0.007	142.9
Sculpin 5–8 cm	1	3.0	0.33
Sculpin 8 cm or over	1	4.0	0.25
Insects			
Grass caddis cases & larvae	772	0.18	5.6
Large gravel cases & larvae	228	0.17	5.9
Small gravel cases & larvae	16	0.03	33.3
Adult caddis flies	81	0.09	11.1
Small caddis flies	92	0.011	90.9
Mayfly nymphs	56	0.068	14.7
Blowfly larvae	88	0.048	20.8
Blowfly adults	3	0.067	15.0
Small beetles	34	0.037	27.0
Large beetles	11	0.18	5.6
Green caterpillars	8	0.062	1.6
Midge larvae	70	0.004	250.0
Midge adults	210	0.001	1000.0
Sandfly larvae	220	0.004	250.0
Sandfly adults	85	0.002	500.0
Other			
Large pond snails	152	0.08	12.5
Small pond snails	570	0.05	20.0
Small planorbid snails	1070	0.013	76.9
Pea clams	146	0.018	55.5
Leeches	6	0.70	1.4
Trash items			
Large stones	88	0.55	1.8
Small stones	168	0.11	9.0
Elderberries	102	0.05	20.0
Bits of twigs, grass, etc.	31	0.10	10.0
Parasites eaten	103	0.008	125.0

Food studies

Method of examination of specimens

Charrs for this study were collected by the various methods just described, from April to September of 1939, 1940 and 1941 from three general areas: 1) Karluk Lake; 2) the mouth of the Karluk River; and 3) Karluk Head to Uyak Bay.

All the charrs captured were taken for tagging or marking purposes – or for examination for tags or marks. If the captured fish were not liberated as tagged or marked specimens, I collected their carcasses for examination. Only a small percentage of the fish caught were actually tagged, and, as thousands of charrs had to be captured to obtain a few hundred tag recoveries, thousands of freshly caught charrs were available for the above studies.

Methods of presentation and analysis of the food data collected

Samples of typical countable food items were collected and preserved in separate containers for later volumetric measurement and counting. Volumetric displacements of such countable food items are presented in Table 2. Most of the volumetric data presented were derived by applying these figures to the counts and estimates made in the field.

As we could not count all of the food items, and as many of the countable items varied greatly in volume among their own kind, we had only two units of measurement available for application to all items: one of quantity (volume in cubic centimeters expressed as 'V' in the tables), and one of quality or availability (frequency of occurrence – or the number of fish selecting the particular item – expressed as 'F' in the tables).

Results

A graphical summary of the length-frequency distributions of charrs examined for food at Karluk Lake is presented in Figure 8. Originally four tables were prepared showing the stomach contents of 636 juvenile and 1,929 adult dolly varden and 103 juvenile and 1,889 adult arctic charr collected in the Karluk Lake area, by months and types of gear employed. However, because of their voluminous nature, they will not be incorporated here. Instead, the data from these four basic tables have been combined and are presented in Tables 3–5. The basic essentials of each of these three tables have been focused into the nine diagrams (Fig. 9) to permit the reader to obtain a quick grasp of the over-all charr food situation as we found it at Karluk Lake, Alaska over 40 years ago.

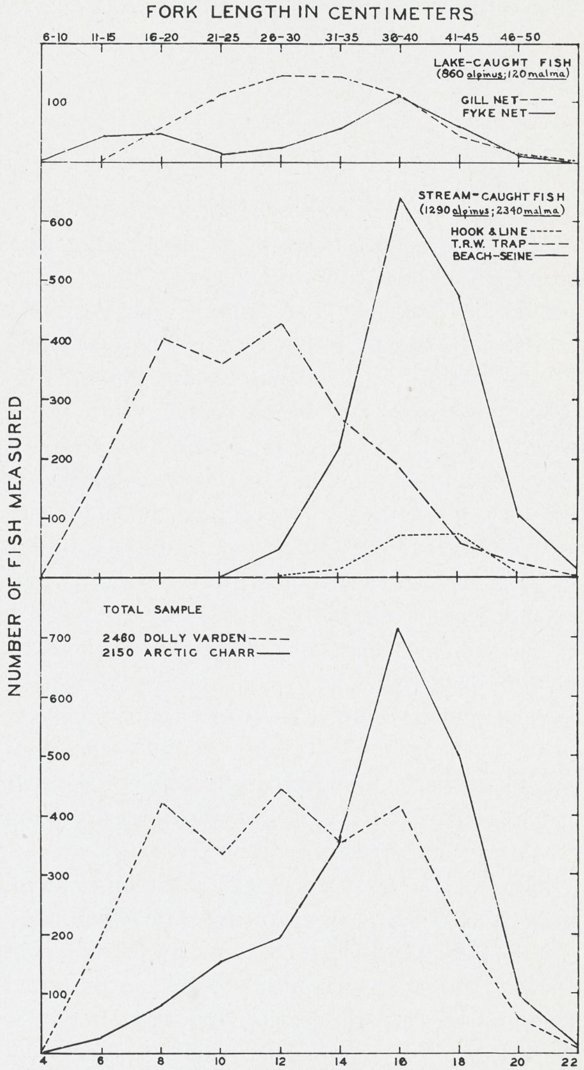

Fig. 8. Length-frequencies of charrs examined for food at Karluk Lake.

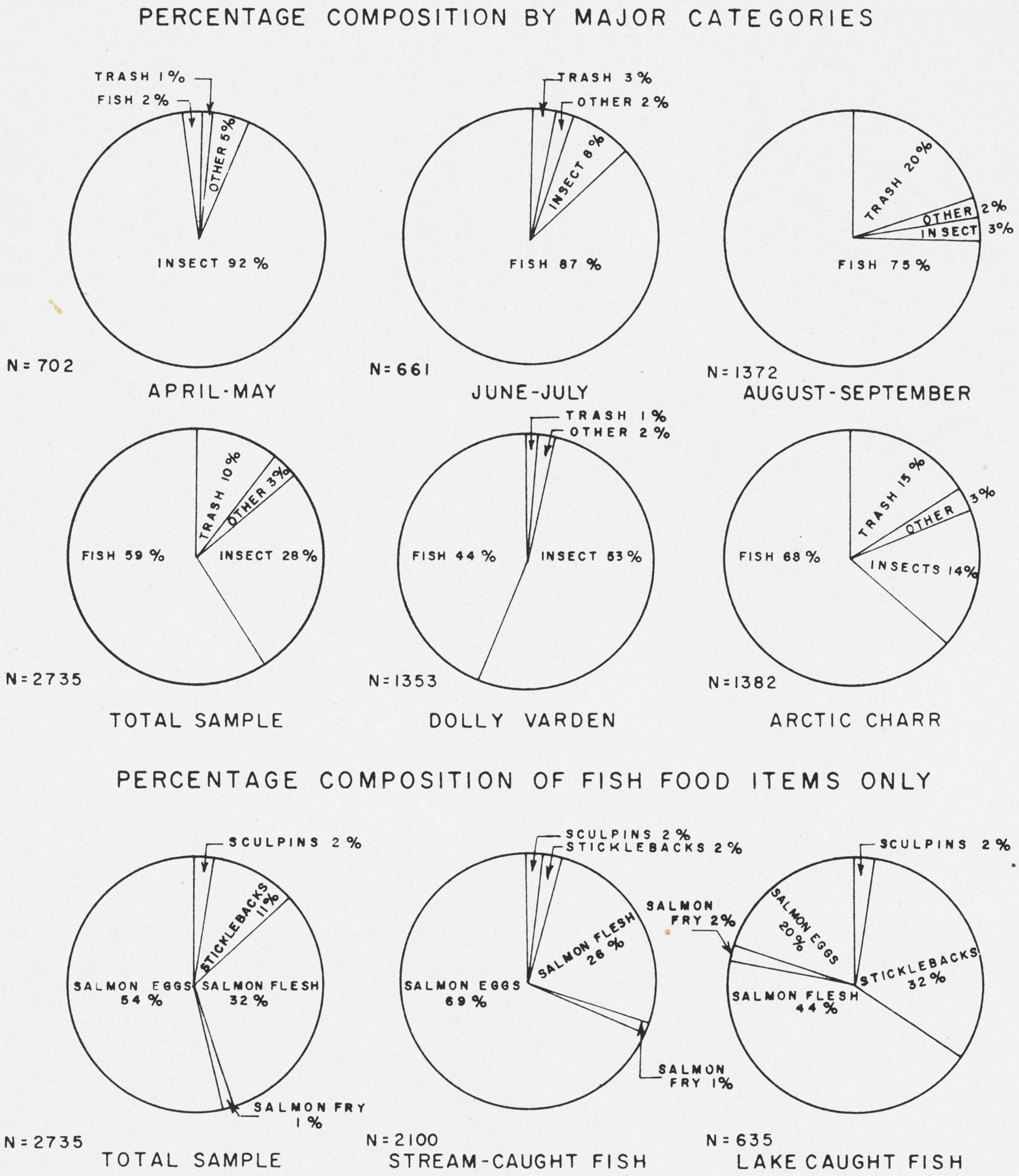

Fig. 9. Natural diets of charrs at Karluk Lake, Alaska, from 1939 through 1941.

On the number of empty stomachs encountered

Stomachs recorded as empty were obsolutely clean of any substance. Tables 3 and 4 indicate that 60% of the charr stomachs examined at Karluk Lake contained at least some trace of food, and 40% were empty. Fish taken by active gear, i.e., by angling and beach seine, showed 90% and 75% respectively of their stomachs contained food. Obviously these fish were actively seeking food when hooked, and the seine hauls made off the mouths of streams were only successful while food items were being dislodged by spawning salmon in those streams. In one case where hauls were made

Table 3. The comparative occurence of five general food classes by months at Karluk Lake.

	April		May		June		July		August		September		Totals	
Number examined														
alpinus	96		89		310		411		442		644		1992	
malma	360		394		30		352		721		708		2565	
Totals	456		483		340		763		1163		1352		4557	
Number and % with food														
alpinus	78	81%	61	69%	211	68%	330	80%	345	78%	357	55%	1382	69%
malma	307	85	256	65%	25	83%	95	27%	234	32%	436	62%	1353	53%
Totals	385	85%	317	65%	236	69%	425	56%	579	50%	793	59%	2735	61%
Fish items	V	F	V	F	V	F	V	F	V	F	V	F	V	F
Salmon eggs														
alpinus	0	0	0	0	100	29	1859	190	676	119	534	95	3169	433
malma	0	0	0	0	27	6	518	68	722	171	1643	397	2910	642
Totals	0	0	0	0	127	35	2377	258	1398	290	2177	492	6079	1075
Salmon flesh														
alpinus	0	0	0	0	23	6	1136	99	1350	146	963	90	3472	341
malma	0	0	0	0	10	2	15	3	26	12	10	2	61	19
Totals	0	0	0	0	33	8	1151	102	1376	158	973	92	3533	360
Juvenile salmon														
alpinus	10	2	0	0	0	0	23	2	10	2	62	7	105	13
malma	1	2	1	2	0	0	1	1	34	7	0	0	37	12
Totals	11	4	1	2	0	0	24	3	44	9	62	7	142	25
Sticklebacks														
alpinus	48	5	10	2	286	63	583	73	43	5	278	45	1248	193
malma	3	1	0	0	1	1	5	1	0	0	0	0	9	3
Totals	51	6	10	2	287	64	588	74	43	5	278	45	1257	196
Sculpins														
alpinus	33	8	0	0	18	2	11	2	60	7	114	29	236	48
malma	0	0	0	0	4	1	0	0	3	1	4	1	11	3
Totals	33	8	0	0	22	3	11	2	63	8	118	30	247	51
Total fish items														
alpinus	91	15	10	2	427	100	3612	366	2139	279	1951	266	8230	1028
malma	4	3	1	2	42	10	539	73	785	191	1657	400	3028	679
Totals	95	18	11	4	469	110	4151	439	2924	470	3608	666	11258	1707
Total insect items														
alpinus	1049	69	238	47	157	135	155	108	45	28	99	96	1743	483
malma	2210	330	1117	263	94	40	37	39	80	62	46	88	3584	822
Totals	3259	399	1355	310	251	175	192	147	125	90	145	184	5327	1305
Total other food items														
alpinus	53	9	66	14	31	43	44	17	45	12	123	65	362	160
malma	115	51	11	9	16	1	0	0	5	2	1	2	148	65
Totals	168	60	77	23	47	44	44	17	50	14	124	67	510	225
Total trash items														
alpinus	18	9	15	17	42	58	102	114	1297	263	337	138	1811	599
malma	4	8	11	12	1	2	12	23	17	51	13	70	58	166
Totals	22	17	26	29	43	60	114	137	1314	314	350	208	1869	765

(Table 3 continued)

Total volume and frequency of all items														
alpinus	1211	102	329	80	657	336	3913	605	3526	582	2510	565	12146	2270
malma	2333	392	1140	286	153	53	588	135	887	306	1717	560	6818	1732
Totals	5344	494	1469	366	810	389	4501	740	4413	888	4227	1125	18964	4002

Table 4. The comparative occurrence of five general food classes among stream and lake-caught charrs by the various types of gear employed at Karluk Lake.

	Stream-caught fish									Lake-caught fish								
	Hook & Line		Beach seine		Thumb weir trap		Total & %			Fyke net		Gill net		Total & %			Grand total & %	
Number examined:	184		1374		2003		3561			374		622		996			4557	
Number and % with food:	165	90%	1031	75%	904	45%	2100	59%		243	65%	392	63%	635	64%		2735	60%
	V	*F*	*V*	*F*	*V*	*F*	*V*	%	*F*	*V*	*F*	*V*	*F*	*V*	%	*F*		
Fish items:																		
Salmon eggs	567	98	2761	292	2086	601	5414	68.5	991	1	1	665	83	666	19.8	84		
Salmon flesh	469	55	1427	110	138	27	2034	25.8	192	23	4	1476	164	1499	44.6	168		
Juvenile salmon	0	0	25	4	46	13	71	0.9	17	21	3	50	5	71	2.1	8		
Sticklebacks	68	15	118	33	6	3	192	2.4	51	835	114	229	31	1064	31.7	145		
Sculpins	28	4	145	29	15	4	188	2.4	37	17	5	42	9	59	1.8	14		
Total fish items	1132	172	4476	468	2291	648	7899	58.2	1288	897	127	2462	292	3359	62.3	419		
Total insect items	91	72	4124	747	666	348	4881	36.0	1167	397	108	49	30	446	8.3	138		
Total other food items	*27*	*10*	*256*	*106*	*29*	*16*	*312*	*2.3*	*132*	*111*	*47*	*87*	*46*	*198*	*3.7*	*93*		
Total trash items	50	61	341	159	90	204	481	3.5	424	96	82	1292	259	1388	25.7	341		
Total all items	1300	315	9197	1480	3076	1216	13573	— 100%	3011	1501	364	3890	627	5391	— 100%	991		

across the mouth, and off the beaches at each side of the Lower Thumb River, a much higher percentage of empty stomachs was recorded among the fish taken in the side hauls.

Although all stationary gear types were examined and cleaned every 24 hours or oftener, fish taken by stationary gear such as fykenet, gillnet, and weir trap showed 65, 63, and 45% respectively of their stomachs contained food. In these situations many fish were just moving through the area when captured, and of those who may have been feeding just prior to their capture, an unknown number could be expected to have lost part or all of their stomach contents by digestion and occasionally by regurgitation during the period of their confinement in the gear. The percentage of empty stomachs from fish captured in stationary gear set in lacustrine waters was fairly uniform at about 35%. This figure reached 55% among fish taken from the stationary Thumb River weir trap. Assuming these fish had fed to some extent before entering the trap, the increase in percentage of empty stomachs was probably due to the increased metabolic rate produced by their ceaseless struggle against the current of water passing through the wire-screen walls of the trap confining them.

Table 3 indicates that 70% of all adult arctic charrs examined at Karluk Lake contained food, whereas only 50% of all adult dolly varden contained food. Roos (1959) found 53% of the 5,050 dolly varden stomachs he examined at Chignik, Alaska, were empty. The more intensive feeding of the arctic charr can be explained, in part at least, by the fact that the adult dolly varden, being anadromous at Karluk Lake, did most of its feeding at sea; while the adult arctic charr, which is not ana-

Table 5. The comparative occurrence of detailed food items among 1,992 arctic and 2,565 dolly varden charrs at Karluk Lake, regardless of time, place, or method of capture.

	S. alpinus			*S. malma*		
	V	%	F	V	%	F
Fish items found						
Red salmon eggs	3084.7	37.5	421	2911.4	96.1	642
Red salmon flesh	3471.5	42.3	341	61.7	2.0	19
Sticklebacks	744.5	9.1	101	3.6	0.1	2
Stickleback eggs	503.3	6.1	92	5.0	0.2	1
Sculpin	205.0	2.5	41	10.8	0.4	3
Pink salmon eggs	83.5	1.0	12	—	—	0
Silver salmon juveniles	59.0	0.7	6	33.6	1.1	7
Sculpin eggs	30.9	0.4	7	—	—	0
Red salmon juveniles	21.0	0.2	1	1.5	tr.	4
Charr juveniles	13.5	0.1	3	—	—	0
Unidentified juveniles	12.5	0.1	3	1.2	tr.	1
Total fish food	8229.4	67.6	1028	3028.8	44.5	679
Insect items found						
Adult insects:						
Caddis fly	20.8	70.0	28	8.4	11.5	9
Midge fly	0.9	3.0	3	19.2	25.3	21
Black fly	1.3	4.0	12	20.9	27.5	7
Blow fly	0.1	tr.	1	1.5	2.0	10
May fly	0.0	None	0	19.2	25.3	4
Crane fly	3.4	11.3	8	0.7	1.0	5
Beetles	3.5	11.7	19	5.9	7.4	15
Totals	30.0	—	71	75.8	—	71
Larval insects:						
Caddis fly	318.0	83.4	101	55.9	44.4	39
Midge fly	2.1	0.6	13	18.5	14.5	28
Black fly	0.4	tr.	8	27.6	21.7	19
Blow fly	43.3	11.3	74	15.8	12.4	20
May fly	11.5	3.0	22	8.8	7.0	5
Crane fly	5.4	1.4	8	0.0	None	0
Butterfly	1.5	0.3	9	0.2	tr.	1
Totals	382.2	—	235	126.8	—	112
Unclassified insects	1335.5	—	177	3390.4	—	639
Total insect food	1747.7	14.4	483	3593.0	52.5	822
Other items found						
Leeches	6.2	2.0	7	60.1	40.9	26
Pea clams	0.8	tr.	4	1.5	1.0	11
Orb snails	162.0	44.8	54	4.6	3.1	1
Pond snails	76.1	21.0	75	16.1	11.0	2
Unclassified snails	116.8	32.2	19	65.1	44.0	25
Total other foods	361.9	3.0	159	147.4	1.0	65
Trash items found						
Inorganic trash	274.9	15.2	280	51.1	89.6	142
Organic trash	1535.9	84.8	318	5.9	10.4	24
Total trash food	1810.8	15.0	598	57.0	2.0	166
Total all items	12149.8	100.0	2268	6826.2	100.0	1637

dromous at Karluk Lake, had to derive all of its growth and sustenance from whatever it could find at Karluk Lake.

On fish food items

The only vertebrate food items available to charrs at Karluk Lake during the period of study were other fishes or their eggs. Fish food items constituted 59% of the entire diet of both species of charrs; 58% of the diet of stream-caught fish; and 62% of the diet of lake-caught fish. However, in a breakdown of total foods consumed by each species, fish items formed 68% of the diet of the arctic charr and only 44% of the diet of the dolly varden at Karluk Lake.

The breakdown of fish food items for both species of charr, as shown in Figure 9, indicates 54% of these fish food items was composed of salmon eggs. In Table 5, where specific fish food items are listed in the order of importance or occurrence, it will be noted that red salmon eggs formed 96% of the fish diet of the dolly varden and only 38% of the fish diet of the arctic charr. Two reasons for this difference were quite apparent: 1) dolly varden generally inhabited streams entering the lake where and when drifting salmon eggs were by far the most available and desirable food to be found and 2) catch records and other evidence presented earlier indicate that the dolly varden practically deserted the lake in late spring, when it migrated to the sea to feed voraciously for two months or more before returning in late summer or early fall in very fine and fat condition preparatory to spawning.

In contrast, the nonanadromous arctic charr, which had remained in the lake, took on during mid-summer a most vile-smelling diet of old testes, eggs, fins, faded flesh and bones torn from the senescent spawned-out red salmon carcasses washed downstream into the lake, mixed with an almost equal volume of moss, algae and other vegetable debris. On this diet it did not appear to be able to approach the superior physical condition so obvious in its anadromous cousin *S. malma*. Although salmon flesh consituted 45% of the fish diet of the arctic charr, it was seldom found in dolly varden stomachs. On the very few occasions when it was, the flesh appeared fresh, pink or red in color, and probably originated as scraps or small remnants of flesh from the feeding activities of the ever-present Kodiak bears during the red salmon spawning season.

The next fish food item of importance is three-spined stickleback (*Gasterosteus aculeatus*) and its eggs, and the aleutian sculpin (*Cottus aleuticus*), which formed the remainder of the arctic charr's fish diet at Karluk Lake. These items appeared in only two dolly varden stomachs probably because of the dolly's tendency toward stream habitation, where it obtained sufficient nourishment from insects in the spring and salmon eggs in the summer and fall; and its general migration to the sea where it fed on marine organisms in the summer.

The only cases of cannibalism observed were the three listed in Table 5 and they occurred when adult arctic charr had been taken by fykenet in which young *S. alpinus* were also captured. We have no record of a similar occurence in *S. malma*.

Some observers have expressed the belief that the dolly varden would dig salmon eggs out of the gravel, if necessary, to obtain them for food. Such activity has never been observed by this writer, and at Karluk Lake it would have been unnecessary because of the large number of salmon eggs drifting downstream during the peak of the red salmon spawning activity. These drifting eggs had been dislodged by new spawners digging new redds over areas seeded by earlier arrivals.

I saw quarts of red salmon eggs massed behind large boulders in spawning streams. These eggs were eagerly devoured by gulls, ducks (including mallards) and mergansers, and occasionally by bears and bald eagles, and silver salmon, rainbow trout, and sculpins. Charr juveniles began eating them as soon as they could open their mouths wide enough to engulf a red salmon egg. Salmon eggs were found in small numbers in some of the adult salmon stomachs. The only fish at Karluk that did not contain salmon eggs was the three spined stickleback. The mouths of even the largest stickleback specimens captured were not large enough to engulf the red salmon eggs.

An actual count from a pint of salmon eggs taken from charr stomachs in 1939 indicated that 17% of the eggs were 'eyed'. A similar quantity of drifting eggs from the same stream at the same time when counted indicated that 20% of them were eyed. It was concluded that the feeding on eggs was a 'scavenger' action and could not in any sense be considered a 'predatory' one, as practically all of these unburied eggs were doomed to destruction whether or not they were consumed.

Juvenile red salmon were found in only five of the several thousand charr stomachs we examined at Karluk Lake. An examination of some 25 red-breasted mergansers taken from the middle of the lake as well as along the shore for parasitological studies revealed only stickleback remains in their stomachs. We could not find nor capture any quantity of these little salmon in the lake, and apparently neither could the charrs nor the mergansers we examined. DeLacy and Gilbert made a special effort to arrive at Karluk Lake early in April of 1940 to collect as many stomachs as possible from charrs captured in or off the mouths of streams where it was known that red salmon alevins were emerging from the gravel and moving down these streams to the lake at night. Only two dolly varden and two arctic charr stomachs were found to contain one alevin each out of 456 charrs examined. Almost 90% of these charrs' food was composed of insect items.

Insect food items

Insect food items constituted 28% of the entire diet of both species of charr. Insects formed 53% of the natural diet of the dolly varden and only 15% of the natural diet of the arctic charr at Karluk Lake.

Except for caddis fly cases, charr stomachs seldom contained only one form or species of adult or larval insect. Adult insects especially were usually found mixed with other food items, and were so difficult to identify, as well as to estimate in number, that they were set aside and the volume estimated of the 'Unclassified' insect material present. Therefore about the only inference that can be drawn from Table 5 is that caddis fly cases or larvae comprised 32% of the dolly varden's and 82% of the arctic charr's insect diet at Karluk Lake. *Eccisomyia* and *Radema* were most frequently encountered in this stage. Adult flies on the other hand, were more common in the dolly varden's diet than in the arctic charr's. If adult insects could be considered as terrestrial forms, they formed only 7% of the arctic charr's and 37% of the dolly varden's diet. The bulk of the dietary evidence indicates these charrs were primarily bottom feeders, although the above evidence indicates that the dolly varden, whose principal habitat is in or near streams, showed a greater tendency to capture insects from the surface than did the arctic charr. The large number of blowfly larvae eaten by the arctic charr was associated with its habit of eating decayed salmon flesh torn from carcasses washed off the shores of the lake or down it affluents during late summer.

The insect material collected from charr stomachs at Karluk has never been submitted to an entomologist for identification, except for the following caddis flies which were identified by D.G. Denning (Stanley G. Jewett, Jr. in lit. 3. 5. 1950): *Glossosoma alascense*, *Chyranda centralis*, *Clistoronia magnifica*, *Psycholglypha subborealis*, *Hesperophylax alaskensis*, *Radema stigmatella*. A published reference to *Eccisomyia conspersa* Banks at Karluk is made by Denning (1951, p. 162).

Other food items

Zooplankton or algae were so seldom observed they were classed with mucus and parasites as trash items. The only microscopic crustaceans observed by the author in any charr stomachs at Karluk Lake were ostracods from the stomach of one very small juvenile dolly varden dipped from a muskeg pond near the O'Mally River. Although other aquatic invertebrates besides insect forms (such as turbellarian and annelid worms) were commonly collected in streams, they were never found in any charr stomachs. Leeches and mollusks were the only other invertebrates besides insects found in charr stomachs at Karluk Lake.

Other food items formed only a fraction of 1% of the natural diet of all charrs examined, and would therefore appear to be comparatively unimportant. Leeches and snails were divided about equally in the dolly varden's 'other invertebrate' diet, while snails comprise 99% of the arctic charr's non-insect invertebrate diet.

Two species of leeches collected were identified by Moore & Meyer (1951) as *Erpobdella punctata* and *Glossiphonia mollissima*. Only *Erpobdella* (sometimes referred to in this paper as the black leech) was found in the 26 *S. malma* and 7 *S. alpinus* stomachs. *Glossiphonia* was found in the shallow waters of Thumb Lake but not in charr stomachs.

The freshwater mollusks from charr stomachs sent to the Smithsonian Institute in 1950 were identified by J.P.E. Morrison (in lit. 25. 5. 1950) as *Sphaerium tenue*, *Pisidium liljeborgii* (listed in Table 5 as 'pea clams'), *Menetus planilatus*, *Valvata leivisii helicoidea* (listed in Table 5 as 'orb snails'), and *Lymnea atkaensis* (listed in Table 5) as 'pond snails').

Trash food items

The term 'trash' (per Ricker 1932) includes all items of doubtful food value. Sand, gravel, stones, mud, and water were termed *inorganic* trash. Bits of moss, wild parsnip seeds, parasitic helminths, mucus etc. were classified as *organic* trash. Trash formed only 5% of the natural diet of all charrs examined, 1% of stream-caught and 24% of lake-caught fish. Ten per cent of all the arctic charr diet and only 0.2 of one per cent of the dolly varden diet was composed of trash. In Table 5 it will be noted that trash items were 98% inorganic in dolly varden and 86% organic in the arctic charr's diet.

Approximately 75% of all the organic trash found in the arctic charr stomachs had a most peculiar origin. Especially during August, when these charrs resorted to a diet of vile smelling, putrid salmon flesh, they usually seemed to 'buffer' it with copious quantities of green algae, moss and mud. Wads of this tangled material which were typical in arctic charr stomachs in late summer were never encountered in any dolly varden stomachs.

Most of these items were believed to be ingested incidentally to regular food items. For example, inorganic items were no doubt scooped up with such bottom foods as caddis-cases, snails or stickleback eggs. But how or why would arctic charrs swallow such large stones as one which measured 2.0 × 2.5 × 3.7 cm, for example, which was taken from a male arctic charr 470 mm fork length caught by fykenet in 4.5 m of water on June 18, 1941. This seems to parallel Kendall's finding (1914) of considerable trash in the stomachs of the lake charr, *Salvelinus namaycush*, and may well indicate that lake charrs are more voracious and less fastidious feeders than are arctic and dolly varden charrs (*S. malma* and *S. fontinalis*). This similarity in feeding habits could be interpreted as further evidence that *S. alpinus* is a connecting link between the lake-spawning charr *S. namaycush* and the stream-spawning charrs *S. malma* and *S. fontinalis* as pointed out by Morton & Miller (1954).

Many of the sticks and bud husks looked like caddis cases, and the red elderberries could easily have been mistaken for salmon eggs. Hairworms (*Gordiacae*) from beetles, and large cestode (*Schistocephalus*) plerocercoids from sticklebacks were eaten incidentally with those food items, but as neither were parasitic to the charrs nor sought as food items per se they were classified as organic trash items.

Results of stomach examinations of dolly varden at the mouth of the Karluk River

Only adult dolly varden charrs were taken at the mouth of the Karluk River or at sea. The feeding habits of *S. malma* during its migrations to and from Karluk Lake are known only from a series of stomach examinations made during May, June and July of 1939 through 1941 at the old Federal salmon-counting weir. The results of these studies are summarized in Table 6 in a manner similar to the foregoing data from Karluk Lake.

From May 26 to 29 and June 8 to 11 in 1939, 2,106 dolly vardens were measured and weighed. They ranged from 18 to 63 centimeters in fork length with an overall average condition factor of 0.799. Of 500 stomachs examined, 400 were absolutely empty and constricted. Only one large charr (52 cm long) had the remains of one red salmon smolt (about 9 cm long) although thousands of smolts were moving downstream at the same time. Thirteen of these charrs had remains of from 1 to 13 pink salmon alevins (about 3 cm long) in their stomachs. Five had egg shells from steelhead still spawning upstream from the weir. Of 159 charrs examined during the same period in 1940 and 1941, 129 or 80% were clean and empty. Four charrs had eaten smolts, a 25 cm charr had 1 pink alevin, a 57 cm charr had 8 red salmon smolts, a 59 cm charr

Table 6. Stomach contents of adult dolly varden charrs (*S. malma*) taken at the mouth of the Karluk River from May through July of 1939–1941 by seine and trap.

	Total downstream migrants (May and June)			Total upstream migrants (July)		
Number of stomachs:						
Examined	659			297		
With food	130 (20%)			30 (10%)		
Empty	529			267		
	V	%	*F*	*V*	%	*F*
Fish:						
red salmon juv.	84.0	–	4	–	–	–
pink salmon juv.	14.7	–	14	–	–	–
silver salmon juv.	2.5	–	1	–	–	–
unidentified juv.	1.5	–	1	–	–	–
steelhead eggs	0.9	–	5	–	–	–
sculpin eggs	0.5	–	1	–	–	–
Total	104.3	47	26	6.0	10	4
Insects:						
adult midge fly	0.01	–	1	0.06	–	5
adult beetles	0.04	–	1	–	–	–
larval caddis fly	35.6	–	20	1.0	–	2
larval midge fly	38.5	–	50	0.03	–	2
larval may fly	3.2	–	17	1.4	–	3
unclassified	2.2	–	0.7	5.0	–	5
Total	79.6	36	96	7.5	13	17
Other invertebrates:						
marine isopods	–	–	–	3.3	–	1
marine amphipods	–	–	–	11.5	–	4
parasitic nematodes	–	–	–	15.2	–	7
Total	–	–	–	30.0	51	12
Trash						
inorganic	26.2	–	21	6.0	–	2
organic	12.4	–	30	9.0	–	3
Total	38.6	17	51	15.0	26	5
Grand total	222.5		173	58.5		38

had 10 red salmon and 1 silver salmon, and a 60 cm charr had 2 red salmon smolts in its stomach.

Among the few downsteam migrating dolly varden charrs that had been feeding, approximately 62% of their diet was composed of insects, 22% of fish food items and 16% of trash. Insect items appeared to dominate their diet as they moved downstream to the sea, as they had at Karluk Lake earlier in the spring. The lack of feeding, the very poor condition factor which is apparent in Figure 6 gave me the impression that these charrs were all 'sick' until they reached the brackish estuary. This sickness is due to the difficult physiological transition that has to be made in brackish water to survive the reversal of osmotic conditions in moving from fresh to salt water. I recall seeing one large dolly varden at the village of Karluk in the lower end of the tidal zone which was quite distended from gorging itself on pink salmon smolt. Apparently once they have adjusted to their osmotic transition they probably join the host of marine predators that await these schools of salmon smolts which may be in some distress as they pass from fresh to salt water. We found smolts in the stomachs of *Leptocottus armatus* and starry flounders at the weir-site. However, only a few of the largest dolly vardens were observed to feed on young salmon before they reached brackish water.

The only stomach samples of upstream-migrating dolly vardens were obtained in July of 1940 when 297 were examined, of which only 10% contained any food. Their diet was composed of 22% insects, 61% other invertebrates, 13% trash and 4% fish food items probably picked up in the brackish estuary of the river. Apparently these fish cease feeding again while making the transfer from salt to fresh water.

It has frequently been stated by various authors in the Alaskan fishery literature that the dolly varden charr migrates to the sea in the spring with the red salmon smolts in order to feed on them en route, and then returns to fresh water with the adult salmon to feed upon their eggs when they spawn. This general concept (with no published evidence to corroborate it) marked the dolly as one of the salmon's worst enemies, and was mainly responsible for the instigation and development of the bounty system. My evidence indicates that most of the dolly varden had moved from Karluk Lake to the sea before the peak of the spring red salmon smolt migration had been reached. Furthermore, stomach examinations of these charr showed that only a very small percentage were feeding on smolts in fresh water. I had the privilege in 1947 of examining 20 dolly vardens taken from among thousands of pink smolts captured at the U.S. Fish and Wildlife Service weir trap for migrant pink salmon at

Table 7. Stomach contents of adult dolly varden charrs taken at sea.

Number of stomachs	Uyak bay traps July 1937, 1939		Karluk Spit beach-seine June 1940, 1941		Total numbers examined	
Examined	449		12		462	
With Food	16 (4%)		11 (77%)		27 (6%)	
Empty	433		2		433	
	V	*F*	*V*	*F*	*V*	*F*
Fish items						
Ammodytes (sand lance)	47.4	6	112.0	9	159.4	15
Trash items						
Inorganic	20.0	1			20.0	1
Organic			5.0	1	5.0	1
Invertebrate items other than insects						
Isopods	11.0	1			11.0	1
Amphipods	36.0	4			36.0	4
Decapods	92.0	5			92.0	5
Unclass. crustaceans			10.0	1	10.0	1
Annelids (*Neriis*)	10.8	2			10.8	2
Totals	217.2	19	127.0	11	344.2	30

Little Port Water, Alaska, and found only two with smolts in their stomachs. I am, therefore, convinced that at Karluk and at Little Port Water the dolly varden was not a serious predator of salmon smolts during its seaward migration.

Stomach contents of dolly vardens at sea

Data collected in 1937 by DeLacy on stomach contents of dolly vardens from Uyak Bay commercial salmon traps combined with similar data collected in 1939 at Larsen Bay are presented in Table 7. It will by noted that only about 4% of these trap-caught fish contained food, probably due to their being held in the trap for a considerable period of time. Notable among these was one dolly varden with a stomach full of white concretions and gray fluid, and another which contained only tiny larval crabs. Six beach-seine-caught fish were obtained from Karluk Spit by Clark Gilbert in June, 1940, and seven more by me on June 9, 1941. Every one of the latter contained from 1 to 50 sand lances which DeLacy identified as *Ammodytes tobianus personatus* Girard 1856. Seventy-seven per cent of the beach-seine-caught fish contained food. A summary from Table 7 indicates that the food of the dolly varden at sea comprised 78% fish, 21% invertebrates and 1% trash.

Until recently the only other reference to food of the dolly varden at sea known to me was by Townsend (1942) who suggested stomach contents of dolly vardens taken off the Aleutian Islands could be used as a method of collecting larval forms of marine crustaceans and fishes. A paper by Lagler & Wright (1962) indicates very little predation on juvenile salmon at sea by the dolly varden although its diet was mainly of other species of fish.

Summary discussion

Catches of charrs at Karluk Lake from April to September indicated that a great majority of dolly varden charr were captured in streams or off the stream mouths in the lake. For example, at the Thumb River weir trap juvenile dolly vardens outnumbered juvenile arctic charrs 20 to 1 and adults 5 to 1. The arctic charr, on the other hand, dominated gill net, fyke-net and hook and line catches made in the lake by a ratio of 2 to 1 for juvenile and 14 to 1 among adult fish.

Although no gear was available to sample deeper parts of the lake adequately, summary figures from 60 sets of a rigid fyke-net made of very fine mesh and set at various depths in the littoral zone of Karluk Lake indicated a species catch ratio of approximately 1 sculpin to 1 juvenile red salmon to 5 dolly varden (2 juvenile and 3 adults) to 23 juvenile silver salmon to 27 arctic charr (6 juveniles and 21 adults) to 1,055 adult sticklebacks. This emphasizes the great abundance of sticklebacks at Karluk Lake in 1939–1941. The only place in the watershed that we did not find sticklebacks was above the high falls in tributary streams to the lake.

The Thumb River weir trap was the most efficient device for capturing dolly varden at Karluk Lake. However, it was selective of small fish, and the least satisfactory for food studies because of the rapid food loss due to the confinement of the fish in moving water.

Angling with hook and line was the least satisfactory gear emplyed to capture charrs at it was usually too time consuming, too undependable and selective of large fish. It was especially useful, however, in capturing tagged charrs from the midst of large school of adult red salmon congregated off stream mouths at Karluk Lake.

Beach seine hauls produced more fish with food in their stomachs than any other type of gear employed except hook and line. It is also worthy of note that practically no sculpins, sticklebacks, or juvenile salmon or charrs ever were found in these beach seine hauls made on concentrations of adult charrs feeding off the mouths of streams, although they mixed quite freely elsewhere in the lakes and streams.

The two gill nets available were in very poor condition and therefore were not fished much. As the fine-meshed end of the experimental gill nets used by the author in subsequent work on trout have never captured significant numbers of small fish, he always has considered these nets selective of large fish. A fleet of gill nets set in the deep waters of Karluk Lake might have produced some interesting results.

The rigid fyke-net was the most unselective gear at our disposal at Karluk Lake. It was the only device by which we were able to obtain a complete series of juvenile arctic charr, and it gave a fairly good cross section of the comparative fish stocks inhabiting the lake bottom in the littoral zone.

At the salmon-counting weir at the mouth of the Karluk River, only adult dolly varden were observed. Practically no juvenile charrs were taken or seen. The few arctic charr observed among them showed no ability to acquire the smolt-like appearance of the habitually anadromous adult dolly varden charr and the juvenile red salmon smolts.

Most of the dolly varden smolts had moved out to sea before the red salmon smolts appeared in large numbers at the weir. The downstream movement of the dolly varden in the Karluk River peaked before the middle of May, whereas the red salmon smolt migration usually peaked in late May or early June. During this period in late May when thousands of adult chinook salmon and hundreds of thousands of adult red salmon were moving upstream through the counting gates of the Karluk River weir during the day, and millions of juvenile red salmon smolts were passing through the same weir at night, it is estimated that approximately 500 spawned-out steelhead trout, 2,000 adult dolly varden charrs and 1 arctic charr were captured each week enroute to the sea.

Among the 30,000 dolly vardens captured during their upstream migration through the Karluk River weir in July of 1939, only 2 arctic charr were positively identified among them. Only one arctic charr was found among 5,000 dolly vardens captured from salmon traps in the sea in July of 1939.

Salmon-trap catches at sea during the summers of 1937–1939 which were examined for charrs showed a ratio of approximately 1 king salmon to 14 silver salmon to 20 dolly varden to 50 dog salmon to 170 red salmon to 810 pink salmon in that general vicivity at that time.

A total of 4,557 charr stomachs were examined at Karluk Lake; 956 at the old Karluk River weir site, and 462 at the salmon cannery at Larsen Bay. All of these fish were collected between May and September, inclusive, of 1938, 1939, 1940 and 1941. A total of 1,919 adult and 636 juvenile dolly varden, and 1,889 adult and 103 juvenile arctic charr stomachs were examined at Karluk Lake. The 1,418 charr stomachs examined at the salmon cannery and the Karluk River weir were all dolly vardens.

Sixty percent of all stomachs examined at Karluk Lake contained food. The percentage varied with the type of gear employed, ranging from 45% at the Thumb River weir, to 65% in gill net or fyke-net catches, to 75% in beach seine hauls and 90% of the fish taken with hook and line.

Over 90% of the charrs' diets during April and May at Karluk Lake was composed of insects. Red salmon eggs and flesh constituted 86% of their diet from June through September. The latter feeding could not be considered of a predatory nature but more of a scavenger type.

Two items, 1) pieces of testes, ova, fins, bones and flesh torn from dead carcasses and 2) adult three-spined sticklebacks and their eggs, which were common in arctic charr stomachs, were seldom, if ever, encountered in dolly varden stomachs at Karluk Lake. The only case of cannibalism observed occurred among arctic charr from Karluk Lake. This seemed to indicate that the arctic charr was a more voracious feeder and probably a more serious potential predator of the young salmon, if young salmon were available, than was the dolly varden. This has been borne out by later studies.

The spring movement of dolly varden down the Karluk River peaked before the major run of downstream red salmon smolts occurred. At the time when both fish mixed in the same dense schools, only 4% of the dolly varden stomachs which were examined contained fish food items. When an anadromous strain of dolly varden is en route to the sea it feeds very little until after it has made the necessary physiological adjustment to the salt water, after which it becomes a ravenous fish feeder. Practically all of the cases of recorded predation of dolly varden on salmon smolts in fresh water have occurred when a nonanadromous strain of dollies were involved; and, of course, there are those earlier cases in which all arctic charr were referred to in Alaska as dolly vardens.

The writer knows of no reference in the available literature which will single out the dolly varden as a more serious salmon predator than another predatory species associated with it in the same situation. Furthermore, he can find no basis whatsoever for the popular but unfair discrimination against the dolly varden which once led to the establishment of a bounty which was in effect in Alaska for some twenty years. Published results of subsequent studies by other workers have confirmed this writer's original thesis of 1942 – that the dolly varden charr is no more serious a predator on other fish species than any other species of trout or charr.

Acknowledgements

The author is deeply grateful to A.C. DeLacy, J.T. Barnaby, and P.R. Nelson for detailed assistance in putting this material together; to G.A. Rounsefell, R.F. Shuman, K.H. Mosher, W.E. Ricker, R.E. Foerster and W.H. King for critical suggestions and comments and to Frances S. and Eleanor S. Morton, and Sara M. Barbur for typing and checking the manuscript.

References cited

Barnaby, J.T. 1944. Fluctuations in abundance of red salmon, *Oncorhynchus nerka* (Walbaum) of the Karluk River, Alaska. U.S. Fish. Bull. 50: 237–295.

Bean, T.H. 1891. Report on the salmon and salmon rivers of Alaska, with notes on the conditions, methods, and needs of the salmon fisheries. Bull. U.S. Fish Comm. (1889) 9: 165–208.

Cobb, J.N. 1930. Pacific salmon fisheries. Rept. U.S. Comm. Fish. for 1930. App. XIII. U.S. Bur. Fish. Doc. 1092: 409–704.

DeLacy, A.C. 1943. Contributions to the life histories of two Alaskan chars, *Salvelinus malma* (Walbaum) and *Salvelinus alpinus* (Linnaeus). Ph.D. Thesis, University of Washington. 114 pp.

DeLacy, A.C. & W.M. Morton. 1943. Taxonomy and habits of the charrs, *Salvelinus malma* and *Salvelinus alpinus* of the Karluk drainage system. Trans. Amer. Fish. Soc. 72: 79–91.

Denning, D.G. 1950. Records and descriptions of nearctic caddis flies Part. III. Journ. Kansas Entomological Society 24: 162.

Gilbert, C.H. & W.H. Rich. 1927. Investigations concerning the red salmon runs to the Karluk River, Alaska. Bull. U.S. Bureau of Fisheries 43: 1–69.

Greenbank, J. & P.R. Nelson. 1959. Life history of the threespine stickleback *Gasterosteus aculeatus* Linnaeus, in Karluk Lake and Bare Lake, Kodiak Island, Alaska. U.S. Fish. Bull. 59: 537–559.

Higgins, E. 1938. Progress in biological inquiries 1937. U.S. Bur. Fish. Administrative Report 30: 31–35.

Higgins, E. 1939. Progress in biological inquiries 1938. U.S. Bur. Fish. Administrative Report 35: 37–39.

Higgins, E. 1940. Progress in biological inquiries 1939. U.S. Bur. Fish. Administrative Report 39: 41–44.

Juday, C., W.H. Rich, G.I. Kemmerer & A. Mann. 1932. Limnological studies of Karluk Lake, Alaska, 1926–1930. Bull. U.S. Bur. Fish. 47: 407–436.

Kendall, W.C. 1914. The fishes of New England. The salmon family. Part 1: The trout or charrs. Mem. Boston Soc. of Nat. Hist. 8: 1–103.

Lagler, K.F. & A.T. Wright. 1962. Predation of the Dolly Varden, *Salvelinus malma*, on young salmons, *Oncorhynchus* spp. in an estuary of southeastern Alaska. Trans. Amer. Fish. Soc. 91: 90–93.

Moore, J.P. & M.C. Meyer. 1951. Leeches (Hirudinea) from Alaskan and adjacent waters. The Wasmann Journal of Biology 9: 11–77.

Morton, W.M. 1942. The Ecology of two Alaskan charrs as shown by their parasites. M.S. Thesis, University of Washington. 31 pp.

Morton, W.M. 1955. Charr or char – History of a common name for *Salvelinus*. Science 121: 874–875.

Morton, W.M. & R.R. Miller. 1954. Systematic position of the lake trout *Salvelinus namaycush*. Copeia 1954: 116–124.

O'Malley, H. 1920. Artificial propagation of the salmons of the Pacific coast. Bur. Fish. Doc. 879, appendix II to Rept. U.S. Comm. of Fish. for 1919: 11–17.

Ricker, W.E. 1932. Studies of speckled trout (*Salvelinus fonti-*

nalis) in Ontario. Publ. Ontario Fisheries Research Lab. 44: 67–110.

Roos, J.F. 1959. Feeding habits of the Dolly Varden, *Salvelinus malma* (Walbaum) at Chignik, Alaska. Trans. Amer. Fish. Soc. 66: 253–260.

Townsend, L.D. 1942. The occurence of flounder post-larvae in fish stomachs. Copeia 1942: 126–127.

Winn, D. 1920. Survey of spawning grounds, extermination of predatory fishes and birds, Bristol Bay, Alaska, 1920. Printed privately for Bristol Bay Salmon Packers. 14 pp.

Winn, D. 1921. (Exact title and pagination unknown). Printed privately by Arcady Press Co., Seattle for Bristol Bay Salmon Packers.

Winn, D. 1022. Survey of spawning grounds, improvements of streams, destruction of predatory fishes and birds, and enforcement of fishery laws and regulations in Bristol Bay, Alaska. Printed privately by Barber, Seattle, for Bristol Bay Salmon Packers. 24 pp.

Winn, D. 1023. Survey of spawning grounds, improvements of streams, destruction of predatory fishes and birds, and enforcement of fishery laws and regulations in Bristol Bay, Alaska. Printed privately by Pike, O'Neil Co., Seattle, for Bristol Bay Salmon Packers. 34 pp.

Winn, D. 1925. Survey of spawning grounds, improvement of streams, destruction of predatory fishes and birds, and enforcement of fishery laws and regulations in Bristol Bay, Alaska. Printed privately for Bristol Bay Salmon Packers. 15 pp.

Env. Biol. Fish. Vol. 7, No. 1, pp. 111–112, 1982

Translation proposals

A Ukrainian book leads in standard of printing

Eugene K. Balon

Department of Zoology, University of Guelph, Guelph, Ontario NIG 2W1, Canada

V.D. Burdak. 1979. Functional morphology of the scale cover in fishes. Published by the A.O. Kovalevsky Institut of Biology of Southern Seas in 'Naukova Dumka' Press, Kiev. 164 pp. (1000 copies, in Russian, with English table of contents and summary) Price 2 rubl. 90 kop.

Most scientific books (at least in our field) published in the USSR are rather unattractive, on low quality paper and with extremely poor halftones. In contrast, this book presented a succession of pleasant surprises: a glossy jacket with a meaningful design in color; a text profusely illustrated with good line drawings and acceptable halftones; 16 pages of full color diagrams showing the imbrication patterns, the taxa dealt with, key scales and a scheme of imbrication.

The text combines review and original data, mostly concise, except for a few elementary passages. The contents are relevant and novel from both the didactic and scientific points of view.

In addition to the Introduction, Conclusion, Summary, Bibliography, Subject and Species Index there are six chapters: 1. general characteristic of the external skeleton of fishlike chordates and fishes, 2. protective and cryptic function of the external skeleton, 3. external skeleton and locomotory function, 4. external skeleton as an adaptation of boundary-layer control, 5. development of the hydrodynamic function of the external skeleton in ontogeny and phylogeny, and 6. experimental survey of the hydrodynamic function of the scale cover.

Whereas this book, like most from the USSR does not include all of the relevant references (e.g. Breder 1947, 1972) and almost entirely ignores the exciting aspects of scale ultrastructure (e.g. DeLamater & Courtenay 1973a, b, 1974), it is nevertheless an important contribution. Viktoria Dmitryevna Burdak's unique scientific work would be most useful if published as soon as possible in English.

Breder, C.M. 1947. An analysis of the geometry of symmetry with especial reference to the squamation of fishes. Bull. Amer. Mus. Nat. Hist. 88: 321–412.

Breder, C.M. 1972. On the relationship of teleost scales to pigment patterns. Contr. Mote Marine Lab. 1: 1–79.

DeLamater, E.D. & W.R. Courtenay, Jr. 1973a. Variations in structure of the lateral-line canal on scales of teleostean fishes. Z. Morph. Tierre 75: 259–266.

DeLamater, E.D. & W.D. Courtenay, Jr. 1973b. Studies on scale structure of flatfishes. I. The genus *Trinectes*, with notes on related forms. Proc. 27th Ann. Conf. Southeastern Assoc. Game and Fish Comm.: 591–608.

DeLamater, E.D. & W.R. Courtenay, Jr. 1974. Fish scales as seen by scanning electron microscopy. Florida Scientist 37: 141–149.

Y.S. Reshetnikov. 1980. Ecology and systematics of coregonid fishes. Nauka Press, Moscow. 302 pp. (1300 copies, in Russian) Price 3 rubl. 50 kop.

This book was conceived when the late G.V. Nikolsky suggested that the author concentrate on this group of fishes. In the first chapter Reshetnikov reviews Berg's geographical (species, subspecies, natio) and nongeographical (race or ecotype, morph, form, abberatio and monstrositas) taxa in relation to more current ecological forms, population oriented species and the typological species concept. Methods of analysis of mensural and meristic characters are reviewed in detail and the Russian version and interpretation of statistical and cluster analysis given. The chapter ends with a brief note on biochemical methods.

The next chapter deals with the feeding and environment of coregonids in northern waters, i.e. climatic and temperature conditions, characteristics of studied lakes, food availability and feeding conditions, intrapopulation feeding relationships, and feeding in whitefishes with course and fine gill rakers.

Chapter three, on growth and population structure and chapter four on maturation and reproduction integrate data from the literature with the author's own findings. In chapter five classification and interrelationships of coregonids with other salmonoids are reviewed. In turn early ontogeny, morphology, biochemistry, genetics and paleontology are treated. Novel evolutionary relationships are presented, taxa redefined, and keys to genera and species have been constructed.

Chapter six is devoted to a brief description of coregonid genera and species with world distribution maps and with comparisons of characters across the distribution ranges. North American ichthyologists may oppose many of the decisions, but even the most opinionated among them cannot afford to ignore Reshetnikov's synthesis.

The distribution and zoogeography in chapter seven is presented in a most interesting way: the paleogeographical relationships of holarctic systems appear in cladograms based on several indices.

The last chapter integrates the conclusions based on coregonids with those based on other fishes. The preferred oligotrophic ecosystems are treated first, followed by reviews of exploitation, introduction, eutrophication, adaptation and some ecological predictions. The general Conclusion, however, is far too short for the variety of topics handled in the book and there is unfortunately no index. The book is not only a rich source of data but presents some unique methods and opinions. If not translated into English soon, much effort may be duplicated.

Env. Biol. Fish. Vol. 7, No. 3, pp. 193–197, 1982

About the courtship rituals in fishes, but also about a false sense of security given by classification schemes, 'comprehensive' reviews and committee decisions*

Eugene K. Balon

Department of Zoology, College of Biological Science, University of Guelph, Guelph, Ontario N1G 2W1, Canada

Keywords:
Reproductive trends, Guilds, Coelacanth, Roach, *Rutilus rutilus*, Early ontogeny, Egg stages, Mating behavior, Committees

> *Those who lack all idea that it is possible to be wrong can learn nothing except know-how.*
>
> Gregory Bateson (1979)
> in Mind and Nature

Although I am probably overstating the obvious, claims confirmed by recognized authorities tend to be accepted too readily and classification schemes favored by such authorities tend to give a false sense of security. During the struggle for survival in a totalitarian milieu my thinking, no doubt, was infiltrated by permanent disbelief of authority. Since then, I have never learned to tolerate bold claims, irrespective of the powers to be and the number of apostles and their followers. This may explain my personal biases while allowing me to remain a moderate. There will always be a mainstream of thoughts and the majority will adhere rather than innovate. When something is proven 'wrong' it does not mean that it should never have been; it may have been an essential stepping stone or trigger for the 'right' to come. Science is practiced by humans and hence will also have fashions. Just because something is fashionable does not mean it is wrong or irrelevant. Some, probably most, fashions will prove to be dead ends, a few will survive to become the mainstreams of science. My quarrel is with none of the above, but with claims pretending to be or accepted for more than they can be, with syntheses in which essentials have been omitted, and with practitioners of politics in science dictating issues via committees.

My concern, after all, is not unique: 'Many thinkers, seeing that the search for truth is an unending quest, abandon it (in dispair perhaps), and settle for agreement with their fellows. If they are right that it is concensus rather than truth that ought to be aimed for in science, then the picture that emerges (and this picture is pretty explicit in some writtings – for example in Kuhn's) is gloomy. It is not just that there will be pockets of scientists who agree among themselves and disagree with the gangs in other pockets – that often happens – nor just that such rival groups may not understand each other – that too happens. What's particularly

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* Editorial

Received 7.5.1980 *Accepted 26.2.1981*

0378-1909/82/0073-0193/$01.00

gloomy, is that the agreement itself becomes vacuous if it is not constrained by external matters' (Settle 1979, p. 522).

In this editorial I have selected three examples to illustrate my points. These are not necessarily the best ones and you may easily replace them with more fitting examples from your own experience. The coelacanth example casts doubts on classification schemes, my personal experience with roach warns against unjustified generalizations and exemplifies the isolationism of language, which is even better reflected in the third example of false security and the sense of saturated knowledge given by so called 'comprehensive reviews'.

The living coelacanth has never ceased to be a source of fascination to me (e.g. Balon 1977). Therefore, I enjoyed immensely the cause and spirit of Lagios (1979a, b) who daringly questioned the conventional placement of the coelancanth within the Osteichtyes (Romer 1966, Miles 1977, Compagno 1979, Griffith & Pang 1979, Schultze 1980). Lagios (1979b) suggested 'that the sister group of the coelacanth is to be found among the Chondrichthyes. (...) Though soft part morphology cannot be compared among extinct taxa, it nonetheless carries significant weight in any systematic analysis'. There is no question that the attributes Lagios studied indicate an evolutionary trend at variance with the trend based on fossilized characters. Had the 'soft' structures been available instead of fossilized structures and had they been used by recognized or fashionable authorities, Lagios' trend might be now the accepted convention (for similar phenomenon see, e.g., Turner 1974).

The most studied and therefore generally accepted patterns bias the best scholarly conclusions. Claims, once made, are copied from text to text (e.g. the Chinese origin of the common carp, Balon 1974), often long after having been disproven. Reproductive styles of fishes, and especially the ethology of courtship rituals have fared no better. For example, concerning nonguarding open substratum spawners, Keenleyside (1979, p. 98) states: 'Among the group-spawners there is little specialized courtship; males chase, push and butt the female and each other. Gamete release is probably synchronized by tactile and chemical signalling. In pair-spawners, male courtship consists mainly of leading the female towards a suitable site, followed by holding her in a spawning clasp.' My observations lead to different conclusions (Balon 1956, pp. 14–15, repeated in Balon & Holčik 1961, translated and paraphrased here):

In aquarium observations on the breeding behavior of roach, *Rutilus rutilus* (a schooling and group spawning European cyprinid), distinct phases of courtship and mating were observed. The duration of each phase sometimes varied, but in general the early courtship phases were long and the later ones consecutively shorter.

Phase 1. Duration is quite variable and the activities pertaining to this phase can be detected in a weak form long before actual courtship. A male chases a female, biting her on the belly and head, rubbing at her sides, belly and back. Then either both sexes rest and ignore each other, or phase 1′ occurs; rarely does phase 2 follow directly.

Phase 1′. The male swims jerkily among the plants alternately spreading wide then closing the fins. On occasion, all fins are held close against the body, or only the dorsal or pectoral fins are extended and vibrated. The entire phase is reminiscent of the displays by some male birds. During this phase the female roach is motionless or follows the male slowly to the surface. Phase 1′ lasts no longer than 5 minutes and sometimes the pair comes straight to the surface at the end of phase 1.

Phase 2. The female remains motionless with her head at the surface and her tail about 2 cm below. On rare occasions she may turn her right side towards the surface. The male rushes up and presses his right side to her left side. The phase is discontinued if the male fails to come to the female within 5 seconds or if he comes to the right side of the female. The average duration of this phase is 10 seconds.

Phase 3. In the side by side position of phase 2, the pair abruptly turn their right sides to the surface (if not already turned). With spasmic jerks of bodies and caudal fins, the gametes are released. This phase lasts 3 to 5 seconds.

Thereafter, the fish part abruptly for an interphase rest, during which they ignore each other and are motionless, often at the bottom. This interval, close to 1 h in length at the beginning of spawning, shortens at the spawning peak – around noon – to an average of 20 seconds, or is immediately replaced by phase 1.

The basic pattern of this courtship ritual was subsequently confirmed in the field (Balon 1967, pp. 53–54). Furthermore, the effective side of the male's approach varied among individual stocks of roach from different water bodies. Some of this was independently supported by Fabricius (1959).

Therefore, the claims made about the absence of elaborate courtship rituals in nonguarding substrate spawners ought to be considered with caution, an idea Keenleyside (1981) adopted recently himself.

Our present knowledge of courtship ethology is heavily biased towards the most frequently studied groups (e.g. chichlids) and the full evolutionary significance of courtship behaviors (Baylis 1981) could not have been incorporated into the reproductive guild trends (Balon 1975a) to any meaningfull extent.

Pair spawning in an aquarium may differ, however, from group spawning. In roach both spawning behaviors were observed in the field, but due to visibility limits clear phases could not be distinguished. Possibly, the same limitations prevented Randall & Randal (1963) from distinguishing courtship phases in parrotfishes and wrasses, although their descriptions indicate that such may exist, and such were seen in *Clarias gariepinus* by Bruton (1979).

My final example is of a review which purports to be comprehensive – Hempel's (1979) 'Early life history of marine fish. The egg stage'. It shows again that at least in our field of science, language (and/or field of research) isolationism can be more severe than in others. This aspect aside, when explicit claims are made that it was 'the author's wish to make a very exhaustive review of the literature on the early life history of fishes from the time of gonadal development to the appearance of a free-swimming larva', that 'for the North American reader this book provides an unique entry to the rich European literature on this phase of the early life history of marine fish' (Mathisen, in Hempel 1979), and that 'more recent literature has been incorporated in the text' (Hempel 1979, p. xv), one expects at least some of it to be fulfulled. When one finds that even many of the relevant papers in German are omitted (e.g. Heinen 1912, Schach 1939, Flüchter 1970, Pommeranz 1973) and landmark studies from other European countries ignored (e.g. Thomopoulos 1954, Bianco 1969, Delsman 1972, Kryzhanovsky 1956, Perceva-Ostroumova 1961, Rass 1968, Soin 1964, 1977, Dechnik 1973, Yevseyenko 1974, to mention only a few) the integrity of the author and the publisher are at stake. Al as many of the omitted references have been quoted earlier in English literature (Russel 1976). There is no need to elaborate upon the harm such false 'comprehensive' reviews can do to the educational process, progress in research notwithstanding. Those who will be aware of these omissions have no need of such reviews, others will be misled into believing that studies of the early life history of fishes have not advanced beyond the reviewer's selection (seel also Houde 1981).

Many examples come to mind of syntheses which omitted essential parts or of committees and reviews used to reinforce personal views over and above customary scientific communication.

How much useful contribution, for example, can be expected from committees on 'standardization of nomenclature'? Nearly in all cases I know about, conclusions reached in such committees ratify parochial dogmas, many disproven long time ago, rather than contribute to knowledge. Consequently, by false restriction of choices they retard future contributions. After all, variation is an expression of freedom in democracy, of progress in science, of evolution in nature. Who needs dictatorship, standardization, or uniformity? It may well be that time lost to such committees is time lost from independent thinking, reading and associative contemplation (see the concluding motto on p. 197). Some, no doubt, will disagree with me on that. Since it is less important what we approve or disapprove of than what consequences (Skinner 1981) we are able to recognize as results of processes we *try to understand*, the points I want to make may after all not be leading up the garden path. Bold claims based on conformistic averaging are more readily accepted and rewarded, for they conflict less with 'habits' (Koestler 1979, p. 240); they restrict however at best the freedom to change or improve, and cannot replace courageous and spirited formulations of ideas, wrong or right (e.g. Bailey 1980 versus Potter 1980 and Vladykov & Kott 1980). It is not the nomenclature that matters but the clear definitions of the contents given to terms, a truism most frequently misunderstood (e.g. Balon 1975b, 1976, Richards 1976).

At this I rest my case – alas too much has already been said – adding only that this editorial is the last part of an earlier essay now broken into three separate articles. As with my earlier communications only much too late did I realize that a succession of papers is rarely read in the intended order and if each does not stand as an independent piece, grave misunderstandings may arise. I do not know how to avoid these other than by pointing out that the first editorial (Balon 1981a) reviewed the evolutionary trends in reproductive styles and the processes which cause the evolution of trends and patterns, that the second communication revised the classification of reproductive guilds (Balon 1981b) and that this editorial intends to warn against too much trust put into any such reviews or schemes, including or especially my own.

Acknowledgements

This editorial is the last part of a larger essay reviewed by Jeffrey Baylis, Ed Crossman, Christine Flegler-Balon, Robin Mahon, Peter Moyle, and David Noakes, who all felt that the essay attempted to cover too much ground. Among other improvements Peter Moyle suggested to have it developed into three separate papers. I complied and thank all for their criticism and valuable suggestions. For comments on the final draft my thanks go to Christine, David and Robin.

References cited

Bailey, R.M. 1980. Comments on the classification and nomenclature of lampreys – an alternative view. Can. J. Fish. Aquat. Sci. 37: 1626–1629.

Balon, E.K. 1956. Breeding and postembryonic development of the roach (*Rutilus rutilus* ssp.). Biologické práce (SAV, Bratislava) 2: 3–60. (In Slovak).

Balon, E.K. 1967. Fishes of Slovakia, with drawings and photographs by the author. Obzor Press, Bratislava. 418 pp. (In Slovak).

Balon, E.K. 1974. Domestication of the carp *Cyprinus carpio* L. Roy. Ont. Mus. Life Sci. Misc. Pub., Toronto. 37 pp.

Balon, E.K. 1975a. Reproductive guilds of fishes: a proposal and definition. J. Fish. Res. Board Can. 32: 821–864.

Balon, E.K. 1975b. Terminology of intervals in fish development. J. Fish. Res. Board Can. 32: 1663–1670.

Balon, E.K. 1976. A note concerning Dr. Richards' comments. J. Fish. Res. Board Can. 33: 1254–1256.

Balon, E.K. 1977. Early ontogeny of *Labeotropheus* Ahl, 1927 (Mbuna, Cichlidae, Lake Malawi), with a discussion on advanced protective styles in fish reproduction and development. Env. Biol Fish. 2: 147–176.

Balon, E.K. 1981a. About processes which cause the evolution of guilds and species. Env. Biol. Fish. 6: 129–138.

Balon, E.K. 1981b. Additions and amendments to the classification of reproductive styles in fishes. Env. Biol. Fish. 6: 377–390.

Balon, E.K. & J. Holčik. 1961. Breeding and reproduction of some native fishes in aquaria. Akvaristicka ročenka 1961–62: 69–82. (In Slovak).

Bateson, G. 1979. Mind and nature. A necessary unity. E.P. Dutton, New York. 238 pp.

Baylis, J.R. 1981. The evolution of parental care in fishes, with reference to Darwin's rule of male sexual selection. Env. Biol. Fish. 6: 223–251.

Bianco, S.L. (ed.). 1969. Eggs, larvae and juvenile stages of Teleostei. Fauna and Flora of the Bay of Naples, Monograph 38 (originally published 1931–1933 in Italian), Israel Program for Scientific Translations, Jerusalem. 417 pp.

Bruton, M.N. 1979. The breeding biology and early development of *Clarias gariepinus* (Pisces: Clariidae) in Lake Sibaya, South Africa, with a review of breeding in species of the subgenus *Clarias* (*Clarias*). Trans. zool. Soc. Lond. 35: 1–45.

Compagno, L.J.V. 1979. Coelacanths: shark relatives or bony fishes? Occ. Pap. Calif. Acad. Sci. 134: 45–52.

Dechnik, T.V. 1973. Ichthyoplankton of the Black Sea. Naukova Dumka, Kiev. 235 pp. (In Russian).

Delsman, H.C. 1972. Fish eggs and larvae from the Java Sea. Reprint of 1921–1938 articles in Treubia by Linnaeus Press, Amsterdam. 420 pp.

Fabricius, E. 1959. Spawning of the roach. Zool. Rev. 21: 17–26. (In Swedish).

Flüchter, J. 1970. Zur Embryonal – und Larvalentwicklung der Seezunge *Solea solea* (L.). Ber. dt. wiss. Komm. Meeresforsch. 21: 369–476.

Griffith, R.W. & P.K.T. Pang. 1979. Mechanisms of osmoregulation in the coelacanth: evolutionary implications. Occ. Pap. Calif. Acad. Sci. 134: 79–93.

Heinen, A. 1912. Die planktonischen Fischeier und Larven der Ostsee. Wiss. Meeresunters. Abt. Kiel (N.F.) 14: 133–188.

Hempel, G. 1979. Early life history of marine fish. The egg stage. University of Washington Press, Seattle. 70 pp.

Houde, E.D. 1981. Book critique of 'G. Hempel, 1979, Early life history of marine fish. The egg stage.' Env. Biol. Fish. 6: 391–392.

Keenleyside, M.H.A. 1979. Diversity and adaptation in fish behaviour. Springer-Verlag, Berlin. 208 pp.

Keenleyside, M.H.A. 1981. Parental care patterns of fishes. Amer. Nat. 117: 1019–1022.

Koestler, A. 1979. Janus: a summing up. Pan Books, London. 354 pp.

Kryzhanovsky, S.G. 1956. On the development of clupeids. Tr. Inst. Morph. Zhiv. Severtsova 17: 1–255. (In Russian).

Lagios, M.D. 1979a. The coelacanth and the Chondrichthyes as sister groups: a review of shared apomorph characters and a cladistic analysis and reinterpretation. Occ. Pap. Calif. Acad. Sci. 134: 25–44.

Lagios, M.D. 1979b. Reply to the rebuttal of Leonard Compagno 'Coelacanths: shark relatives or bony fishes'. Occ. Pap. Calif. Acad. Sci. 134: 53–55.

Miles, R.S. 1977. Dipnoan (lungfish) skulls and the relationship of the group: a study based on new specimens from the Devonian of Australia. Zool. J. Linn. Soc. London 61: 1–328.

Perceva-Ostoumova, T.A. 1961. Reproduction and development of the Far-East flatfishes. Acad. Sci USSR Press, Moskva. 486 pp. (In Russian).

Pommeranz, T. 1973. Das Vorkommen von Fischeiern insbesondere von Eiern der Scholle (*Pleuronectes platessa* L.) in den oberflächlichen Wasserschichten der südlichen Nordsee. Ber. dt. wiss. Komm. Meeresforsch. 22: 427–444.

Potter, I.C. 1980. The Petromyzoniformes with particular reference to paired species. Can. J. Fish. Aquat. Sci. 37: 1595–1615.

Randall, J.E. & H.A. Randall. 1963. The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. Zoologica 48: 49–60.

Rass, T.S. 1968. Spawning and development of polar cod. Rapp. R.-v. Reun. Cons. perm. int. Explor. Mer. 158: 135–137.

Richards, W.J. 1976. Some comments on Balon's terminology of fish development intervals. J. Fish. Res. Board Can. 33: 1253–1254.

Romer, A.S. 1966. Vertebrate paleontology. 3rd ed., Univ. of Chicago Press, Chicago. 468 pp.

Russel, F.S. 1976. The eggs and planktonic stages of British marine fishes. Academic Press, London. 524 pp.

Schach, H. 1939. Die künstliche Aufzucht von *Clupea harengus* L. Helgol. Wiss. Meeresunters. 1: 359–372.

Schultze, H.-P. 1980. Review of 'The biology and physiology of the living coelacanth'. Syst. Zool. 29: 226–228.

Settle, T. 1979. Popper on 'when is a science not a science?' Syst. Zool. 28: 521–529.

Skinner, B.F. 1981. Selection by consequences. Science 213: 501–504.

Soin, S.G. 1964. Breeding and development of *Limanda limanda* (L.) of the White Sea. Voprosy ichtiologii 4: 495–511. (In Russian).

Soin, S.G. 1977. Study of the developmental principles in marine fishes and their significance for elaboration of biological bases of mariculture. Voprosy ichtiologii 17: 275–284. (In Russian).

Thomopoulos, A. 1954. Sur quelques oeufs planctoniques de Téléostéens de la baie de Villefranche. Bull. l'Inst. Océanogr. 1043: 1–15.

Turner, B.J. 1974. Genetic devergence of Death Valley pupfish species: biochemical versus morphological evidence. Evolution 28: 281–294.

Vladykov, V.D. & E. Kott. 1980. Description and key to metamorphosed specimens and ammocoetes of Petromyzonidae found in the Great Lakes Region. Can. J. Fish. Aquat. Sci. 37: 1616–1625.

Yevseyenko, S.A. 1974. New data concerning eel eggs on Georges Bank. Journal of Ichtyology 14:294–298.

> *... The role of individuals in science is of central importance to its health and progress. (...) Major discoveries are initiated by individuals and modified by a selection process of other individual minds. 'Group' mind does not play a role in this model. I would assert that 'group' mind does not posses sufficient emergent properties in the same sense as 'individual' mind: the latter is open and democratic, whilst the former is closed and authoritarian.*
>
> E.J. Steele (1981)
> in Somatic Selection and Adaptive Evolution.
> The University of Chicago Press.

From: Southeastern Log
Vol. 9, No. 9, September, 1979

Dolly Varden: They're not the villains they're thought to be

By BOB ARMSTRONG
For The Log

Between 1921-1940 more than six million Alaskan Dolly Varden were destroyed under a predator control program. This program, administered by the U.S. Bureau of Fisheries, was begun because Dolly Varden was thought to be a serious predator on salmon eggs and young.

Between 1921 and 1929, the charr were captured, killed and discarded by the U.S. Bureau of Fisheries representatives. Starting in 1930, a reward of five cents for the tail of every Dolly Varden, lake trout and northern pike was offered through funding appropriated by the Territorial Legislature and matched by the Bristol Bay Salmon Packers Association.

The residents of Bristol Bay would catch the fish, dry the tails, assemble them by the hundred on strings and deliver them to a representative of the USBF for payment.

In 1935, the program was further accelerated by the killing of Dolly Varden at several weirs manned by USBF personnel. Shortly thereafter, the program was expanded to Kodiak Island, Cook Inlet and eventually Yakutat.

The bounty was reduced in 1937 to 2½ cents per tail, and in 1941 payment of bounties for predatory fish was discontinued in the Bristol Bay and Cook Inlet regions following the legislature's non-appropriation of funds for the work.

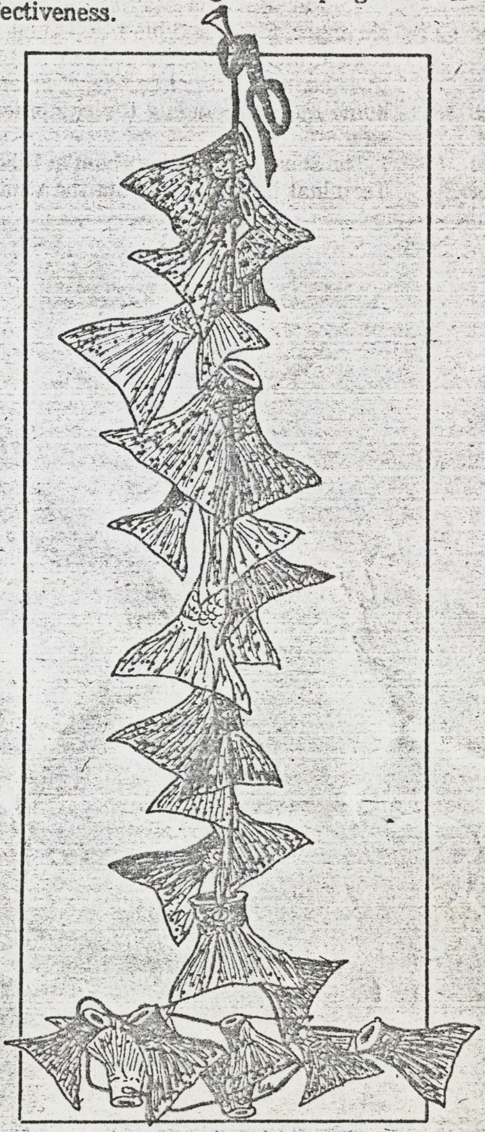
This program may have been one of the greatest boondoggles in the history of Alaska fisheries. Let's examine some of the facts surrounding the program.

—The program was based on little or no research. In other words, no studies were conducted in most areas where Dolly Varden were being removed to even determine if they were feeding on salmon eggs or young.

The only study cited in the literature is an examination of about 100 "Dolly Varden trout in Lake Alegnagik at the mouth of the inlet from Lake Nerka, and of these all or almost all were filled with migrating red salmon fingerlings." Present studies by the Alaska Department of Fish and Game have shown these fish to be non-migratory Arctic char and not the migratory Dolly Varden—the fish most often killed during the program. More on this will follow.

Continued on page 21

—Many, and in some instances the majority of the tails being turned in for bounty were from rainbow trout and salmon—the very species they were attempting to save. It wasn't until 1939, almost 20 years after the program was instigated, that biologists were called in to investigate the program's effectiveness.



Dolly Varden tails brought a nickel each

In the USBF office at Yakutat 20,000 tail samples were examined, all of which were supposedly Dolly Varden. The examination showed that these tails were from 3,760 rainbows, 14,200 coho salmon and only 2,040 Dolly Varden. In Bristol Bay even the "trophy" rainbows of the Newhalen and Naknek rivers were being killed and discarded after their tails were cut off for a bounty of 2½ cents each.

—Many, if not most of the Dolly Varden

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Dolly Varden . . .

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being killed were not predators on salmon young. On Kodiak Island more than half a million Dolly Varden were destroyed at weirs until studies indicated the fish they were killing had not been feeding on salmon young. In contrast, they found the non-migratory Arctic char living in Karluk Lake to be the real culprits that were feeding on salmon young. The biologists' conclusion was that the fish being killed—the migratory Dolly Varden—seldom ate young salmon but that the Arctic char, which did not migrate to sea and was the real culprit, had hardly been touched by the bounty or predator control program except in Bristol Bay.

So much for history. The unfortunate result of this 20-year "predator" control program is that the misinformation and publicity generated has branded the Dolly Varden as a serious predator on salmon eggs and young to this day.

The prejudice leveled against the species still results in predator control proposals being given to the USBF each year and has resulted in one proposal from the Northern Southeast Regional Aquaculture Association to subsidize a commercial fishery for Dolly Varden in Southeast Alaska.

After the predator control program had ended, several studies were conducted to determine the seriousness of the Dolly Varden as a predator on salmon eggs and young.

In a review of more than 400 publications on the Dolly Varden, I could not find a single properly conducted study that indicated Dolly Varden were a serious predator on salmon young. After eliminating a few references because of inadequate sample sizes or an obvious bias in their experimental design—two authors examined stomachs from char caught in a salmon fry trap—I found the following seven studies that appeared to be properly conducted:

CHIGNIK LAKE—Of the 5,050 Dolly Varden examined, 214 had been feeding on salmon young. The author concluded: "...from the evidence obtained they are not serious predators upon the young salmon in the Chignik system."

KARLUK LAKE—Of 3,371 Dolly Varden examined, 21 contained salmon young. The author concluded: "...the seriousness of the Dolly Varden as a salmon predator has often been overstated."

LITTLE PORT WALTER—Of 183 Dolly Varden examined, only four had fed on salmon young.

PERIL STRAITS—Of 3,888 Dolly Varden examined, 25 had fed on salmon young. "...until further evidence is collected, the Dolly Varden should not be considered a serious threat as a predator on salmon young," the author concluded.

AMCHITKA ISLAND—Of 2,513 Dolly Varden examined, none had been feeding on salmon young.

BEAR LAKE—Of 178 Dolly Varden examined, none had been feeding on salmon young.

RUSSIA—Of 529 Dolly Varden examined, only one contained salmon young. The author concluded: "...the char consume smelts and sticklebacks, which are food competition of the young sockeye and thus are more beneficial than harmful."

Several studies showed that Dolly Varden do eat salmon eggs, but they are not eating eggs that would have otherwise survived. When salmon spawn, many eggs wash out of their redds before they can cover them with gravel.

Also, salmon often build their nests over earlier nests, thereby digging up the eggs deposited by other salmon. These drifting, loose eggs are the ones being eaten by Dolly Varden. Some biologists feel the eating of these unburied eggs is beneficial to salmon because otherwise the eggs eventually die and fungus, thereby possibly infecting the live eggs and alevins in the gravel.

Pat of the prejudice problem stems from misidentification of fish species in the literature. For instance, the non-migratory Arctic char of the Wood River lakes in Bristol Bay and at Karluk Lake on Kodiak have been shown to be serious predators on sockeye salmon young at certain times of the year.

In the literature these fish have often been referred to as Dolly Varden, which they are not. Farther south, in parts of British Columbia, Washington and Idaho, the thought-to-be Dolly Varden have been well known for their predator activities on other fish. One classic study at Cultus Lake in British Columbia showed the "Dolly Varden" to be a significant predator on sockeye salmon young. However, recent studies indicate these fish were not Dolly Varden but rather the bull char, a completely different species.

I have spent 10 years conducting research on the sea-run Dolly Varden in Southeastern Alaska. Over this period I have examined thousands of stomachs from fish sampled in the many different habitats frequented by the fish. I have yet to observe a situation of predation on salmon young that could be considered serious.

Mostly, Dolly Varden were found to eat capelin, sandlance, freshwater snails and various invertebrates. However, on occasion

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they do feed on salmon young. During the time pink ad chum fry are leaving streams, Dolly Varden young (smolts) also are migrating to saltwater. These young Dolly Varden do eat the pink and chum, but their size (4-5 inches) allow them to only ingest a few fry per day.

In saltwater I have found occasionally areas where the larger Dolly Varden were feeding on salmon young along with other species of fish. Usually these concentrations of Dolly Varden were small.

Perhaps areas exist in Southeastern where the concentration of Dolly Varden feeding on salmon young are large enough to do significant harm to a population of salmon. However, to my knowledge these areas have not been found. I am convinced that most populations of Dolly Varden in Southeastern are not significant predators on salmon young.

From the evidence collected I can only class them as occasional predators of salmon young, along with other known predators such as cutthroat trout, coho salmon, walleye pollock, Pacific herring, rainbow trout and cottids. Of interest is the fact that some of the preceding species have been shown to be far more voracious predators than the Dolly Varden.

Dolly Varden, in fact, may be beneficial to salmon. Ecological relationships among fish are complex and difficult to understand. For instance, whil in lakes the sea-run Dolly Varden feed heavily on freshwater snails. These snails are a intermediate host of a parasite that infects the eyes of coho and sockey salmon young, eventually causing blindness.

After removal of Dolly Varden from Bear Lake in Seward, large numbers of coho smolts died from this "eye fluke" disease.

At Lake Alegnagik in Bristol Bay, after the predator removal program worked there, biologists found almost all of the migrating red salmon were seriously parasitized by a round worm. They said it is possible that the control of Dolly Varden may have caused the increased parasitization of the salmon. Certainly, the Dolly Varden habit of "cleaning up" the loose salmon eggs in streams reduces the possibilities of fungus spreading to the live eggs and alevins in the gravel.

The competition between Dolly Varden and more serious salmon young predators may also play a role in reducing overall predation of salmon young by all species of fish. I admit that most of this is speculation, but I do feel the evidence gathered to date indicates Dolly Varden may have a beneficial effect on the health of our Southeastern salmon population.

In summary, I can see no benefit whatsoever to an overall cntrol program on Dolly Varden in Southeastern, whether it be in the form of "no bag limits" or under the disguise of a subsidized commercial fishery. Research may determine specific situations where Dolly Varden should be controlled in some way to protect out-migrating salmon.

This may be especially true of pink and chum salmon hatcheries where "unconditioned" fish are released near major concentrations of Dolly Varden. In these instances, special release times or methods such as screening off release areas will be found to minimize predation.

As a last resort, the Dolly Varden could be captured and held until the "danger' period was over. The killing and discarding of Dolly Varden that went on between 1921-40 is, in my opinion, an unthinkable solution.

Over the years, sea-run Dolly Varden have become one of the most important sport fish species in Southeastern. In a recent survey of more than 2,000 anglers from Southeastern, Dolly Varden ranked fourth on a list of the 12 most sought after species. They are obviously no longer considered a "trash" fish, but are now recognized as the "bread and butter" fish of the state and as a species which demands as much care as any other.

(Editor's note: Bob Armstrong is a fishery biologist assigned to the Sport Fish Division, Alaska Department of Fish and Game.)

Here's Dolly

Dolly Varden are one of Alaska's most important and sought-after sport fish. It is unique as it is the only member of the family Salmonidae, excluding salmon, that has readily adapted to the numerous small-to-medium size non-lake streams that enter our saltwater areas.

Good Dolly Varden fising can be found in saltwater during May, June and July. As the mature fish return to their home stream to spawn and feed in August and September, most coastal streams in Southeastern Alaska and up through the Aleutian Chain provide good fishing for Dolly Varden. Try fishing near spawning salmon, in deep holes and at the creek mouth on an incoming tide. Lake fishing for sea-run Dolly Varden can be good from late August through November. The fish begin entering lakes in late August and are in prime condition after their spring and summer growing season. Ice fishing in lakes during the winter also can provide excellent sport.

Dolly Varden flesh is pink, firm and full of flavor. For variety, try smoking some of your catch or cooking them in the hot coals of a beach fire while the fish are wrapped in foil, adding a little butter, salt, pepper and lemon juice.

Dolly Varden will usually strike readily at almost anything an angler offers. Spinning lures or single salmon eggs bounced along the the bottom should produce results in August and September.

(Editor's note: The above information was condensed from ADFG's Wildlife Notebook Series.) sl240

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Dolly Varden

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Morton's pap. Arctic charr / dolly varden / Karluk

- Reproductive guilds (check)

letter re → Larval Symp. paper

From:

E.K. BALON
Department of Zoology
University of Guelph
Guelph, Ontario
N1G 2W1

To:

Dr. Robert J. Behnke
Department of Fishery and
  Wildlife Biology
Colorado State Univ.
Fort Collins, Colo. 80523
U.S.A.

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