*Aquaculture*, 28 (1982) 1—19
Elsevier Scientific Publishing Company, Amsterdam — Printed in The Netherlands 

# MORPHOLOGICAL INDICES OF DEVELOPMENTAL PROGRESS IN THE PARR—SMOLT COHO SALMON, *ONCORHYNCHUS KISUTCH*

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(Accepted 15 January 1982)

## ABSTRACT

Gorbman, A., Dickhoff, W.W., Mighell, J.L., Prentice, E.F. and Waknitz, F.W., 1982. Morphological indices of developmental progress in the parr—smolt coho salmon, *Oncorhynchus kisutch. Aquaculture,* 28: 1—19.

By common usage rather than by strict definition a parr is understood to be a young salmonid with vertical dark stripes, and a smolt is a slightly older and larger fish in which the dark stripes are obscured by a deposition of guanine in the scales and the skin, giving a silvery color. Although parr and smolt remain satisfactory terms for general usage, they are not sufficiently precise to describe the normal genetically based developmental variants in salmon, and certainly they cannot specify or describe the non-synchronous development of young salmon subjected to experimentally altered environments (e.g., special diets, hormonal manipulation, photoperiod, temperature, salinity).

To aid in more detailed description of developmental variants in the parr—smolt transformation a study was made of externally measurable features that change significantly during this period. In addition to pigmentation and length, the following items proved to be useful indices of differentiation: emergence and growth of teeth on the maxilla, mandible and tongue; growth and changes in shape of integumentary folds adjacent to the cloacal opening; growth and change in shape of the auxillary appendage of the pelvic fin; and growth in the scales with respect to radius and number of circuli. These additional features appear to reflect chronological age more faithfully than does integumentary pigmentation. In further studies of experimentally altered parr and smolt, and in normal genetic variants, these features, when related (or not) to differentiating physiological and biochemical properties, should greatly amplify and improve the precision of descriptions of developing salmonids.

## INTRODUCTION

The monosyllabic names parr, smolt, grilse, and kelt apparently had their origins among Scottish and English fishermen and fish culturists of the nineteenth century, or earlier. They have been generally useful terms in distinguishing and recognizing salmonids in various stages of development and reproductive states. In these contexts they remain useful and are frequently employed in the scientific literature.

The adequacy of this classic terminology recently has been brought into question, particularly in certain contexts, when applied to detailed analysis of the development of young Pacific salmon and trout in the parr and smolt stages. In the Northwest, a parr is recognizable as a young salmonid, normally no more than 1.0 to 1.5 years of age, nor more than 120 mm in length, with characteristic dark vertical streaks along its sides composed of concentrations of melanophores. A smolt is a larger and older (1.0 to 2.0 years old) fish in which deposition of guanine in the scales and the skin gives the fish a "silvery" color which obscures the dark "parr marks". Generally, definitions of the smolt infer that this is the form which migrates to the sea. Clearly, in addition to pigmentation, there must be progressive differences in size and behavior that should readily distinguish the parr from the smolt.

More recently, features of a physiological nature have been added to characterizations of the parr-to-smolt transformation, and the entire process has been referred to as "smoltification". Principal additional features are a developed tolerance to seawater, or osmoregulatory ability, and appearance of enzymic activity (ATP-ase) in the gills that is considered to be a part of the osmoregulatory mechanism. Beyond these features, blood plasma levels of thyroid and interrenal corticosteroid hormones, and normal ranges of plasma osmolar concentrations of electrolytes shortly after the fish enter seawater also characterize the normal progression of the parr-to-smolt development (Folmar et al., 1982).

What, then, is the basis for the dissatisfaction with this terminology in current usage? Researchers engaged in experimental analysis and regulation of the parr-to-smolt stages of Pacific salmon development now require more precision in describing these stages than the simple names provide. The addition of qualifying adjectives and prefixes like *early*, *late*, *mid-*, *pre-*, *post-* in general have had limited utility, and have been so poorly defined that different laboratories have no dependable way of communicating to each other equivalence of their definitions.

The traditional basis for definition of smoltifying salmonids, the silvering of the skin due to guanine deposition, has proven easily reversible and not necessarily correlated with size or with developing physiological or biochemical features. Other less readily described integumentary pigmentary changes may be locally useful, but appear to be of little general applicability in different races of the same species. The greatest nomenclatorial difficulties have arisen in experiments in which "normal" development of parr and smolt is altered by manipulation of temperature, photoperiod, environmental salinity, diet, hormonal treatments, etc. A frequent result of such deliberate interventions in the normal process is non-synchronous development in which some features progress (at varying rates), some remain static, and some may even revert to an earlier state. Obviously, reference to "parr" or "smolt" becomes specious under abnormal circumstances, as though separate items in the entire process of development remain locked together even under abnormal circumstances. Workers in this field, under altered circumstances, have used such terms as "stunt" or "revertant" to characterize non-growing undersized young salmonids, or fish in which certain already developed structural or functional features have regressed or dedifferentiated. Desynchronization or separation of normally associated individual features of development are known in experimentally manipulated amphibian embryos. For example, thyroid hormone treatment of tadpoles can produce abnormally proportioned and miniature-sized metamorphosing monsters which generally die.

Naturally occurring variants from the "normal" course of the developmental process in young salmon also impose great terminological difficulties. When dark-colored specimens are found within a given group of silvering smoltifying young salmonids, and if these animals have developed *some* of the physiological properties of smolts, should these be considered parr-like smolt, or partially developed smolt, or an arrested or a reverted parr? Perhaps the most thorough study of developing features of the parr—smolt period is that of Kubo (1974, 1980) who found considerable phenotypic polymorphism in parr as well as smolt stages in a single generation of developing masu salmon (*Oncorhynchus masou*). Using the criteria of body form, size, melanotic pigmentation of the dorsal fin, silvering of the body, behavior, as well as several physiological and biochemical indices, he found it possible to recognize at least five or more types of parr: silvery parr, dark parr, yellowish parr, medium-sized parr, and small parr (see Fig. 1). These contemporary animals were not only distinguishable from each other, but also they differed with respect to their developmental potential. Some fish remained parr for at least another year (permanent stream residents) and some proceeded with what may be defined as "smoltification", which as a rule means completion of the integumentary silvering by their second spring. The masu smolts, as well as the parr, have several possible types. Most of them continue differentiation and migrate to the sea. Some of them, "pseudo-smolts" are considered by Kubo to be derived from smaller "medium-sized" parr, and subsequently revert to the unsilvered parr type and remain in fresh water. Even after arrival in seawater, not all smolts uniformly continue their "normal" progressive development; some of them revert to parr-like pigmentary patterns and possibly return to fresh water.

Is this heterogeneity an expression of "abnormality", or is it a normal expression of genetic differences in a given age-class population of salmonids? Can this be an adaptive phenomenon of differential development which breaks up the contemporary hatch of a particular year into subgroups? The dispersion of a single population into groups of varying developmental rates and geographic distribution reduces the likelihood of destruction of an entire generation through some environmental catastrophe. In animal species in which breeding occurs only once per lifetime, vulnerability to environmental catastrophe that coincides with the breeding period is very real, and, in fact, has been witnessed in sockeye salmon (*Oncorhynchus nerka*) in the Fraser River, B.C. (Netboy, 1974).

In an effort to determine the degree to which genetically based polymorph-

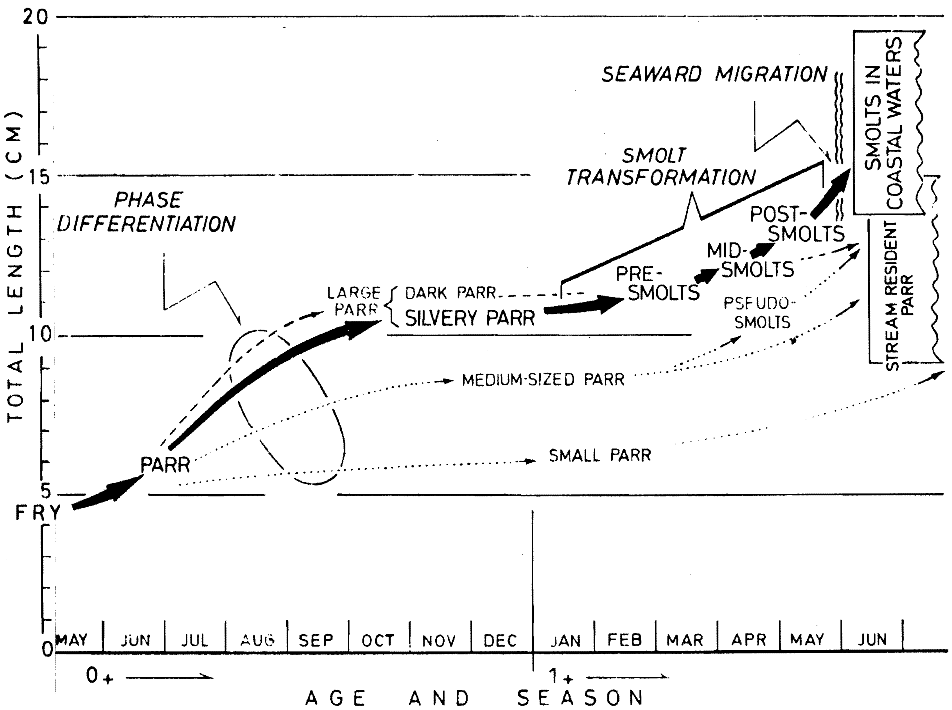


**Fig. 1. Semi-diagrammatic representation of body growth, phase differentiation, and smolt transformation of masu salmon. From Kubo (1974). Note that several types of parr differentiate during their first year of development. These parr have different developmental potentials which are expressed during the smolt transformation (or lack or delay of it) during their second year.**

ism contributes to the difficulty in recognizing "normalcy" in development of parr—smolt coho salmon, we evaluated morphological features that can be used to define stages in such development. One goal in the study was to determine whether the frequently used term "metamorphosis" is applicable to this phase of salmonid development. In a metamorphosis we must assume that a rapid and profound change in form and/or physiological properties occurs during this period. It should be stated that the report of observations we summarize here must be considered an interim one. The major accomplishment of this study has been to provide a procedural basis for characterizing normal and experimentally altered developmental progress in parr—smolt coho salmon. Future studies must examine other populations of *O. kisutch* under varying circumstances before broad generalizations can be justified.

## METHODS AND MATERIALS

Coho salmon used in this study were taken from the Skykomish hatchery of the Washington Department of Fisheries (Startup, WA). The eggs were fertilized in mid-November 1978. In mid-February 1980 the fish were transferred to the Northwest and Alaska Fisheries Center of the National Marine Fisheries Service, Seattle, WA, and were reared in 1.2-m diameter light green cylindrical tanks continuously supplied with dechlorinated municipal water. Rearing density was 24 $kg/m^3$. Ambient temperatures varied between 5 and 15°C. The fish were kept outdoors under natural light and fed Oregon Moist Pellets (approximately 2% body weight/day). Groups of specimens were selected according to pigmentation and were photographed, measured, and sampled for morphological studies at the following intervals: 21 March 1980 (Parr, age approximately 16 months); 11 April 1980 (Transitional, age approximately 17 months); 25 April 1980 (Smolt No. 1 and Smolt No. 2, age approximately 17.5 months); and 30 May 1980 (Smolt No. 3, age approximately 18.5 months). By early June 1980 most of the fish had the external appearance of smolts, and were placed in a seawater net-pen (salinity $29^0/_{00}$) in Puget Sound at Manchester, WA. From this site, they were sampled on 18 August 1980 at about 21 months of age and designated seawater parr, transitional, and smolt according to several visible visual criteria described below.

The selection of specimens was based on visual criteria which included body color, fin color, and the presence or absence of parr marks. The precise characteristics that distinguished the fish in the various groups (Prentice et al., 1981) are as follows.

*Parr*: light brown to yellowish overall color, yellow to brownish-orange fin color, parr marks dark and clearly evident, little or no silvering of scales, and relatively robust in appearance. The ratio of eyeball diameter to its total length ($E : L$) is usually greater in parr stage fish than in other smoltification stages (Fig. 2A).

*Transitional*: parr marks partly obscured because of guanine deposition in the scales, although not completely silvery; fin color becoming clear or uniform light gray; relatively robust in appearance; $E : L$ ratio decreasing from that of a parr (Fig. 2B).

*Smolt No. 1*: parr marks almost completely obscured by the silvery appearance of the scales, fins are clear with slight intensification of black pigment (melanin) at outer edge of dorsal fin and extremities of caudal fin lobes, and fish are relatively thinner in appearance. $E : L$ decreasing.

*Smolt No. 2*: parr marks completely absent, fins clear with greater intensification of black pigment at outer edges of dorsal fin and caudal fin lobes, and fish are slender in appearance.

*Smolt No. 3*: parr marks completely absent, fins clear with very intense black (almost fluorescent) pigment at outer extremities of dorsal fin and caudal fin lobes, and fish are slender in appearance (Fig. 2C).

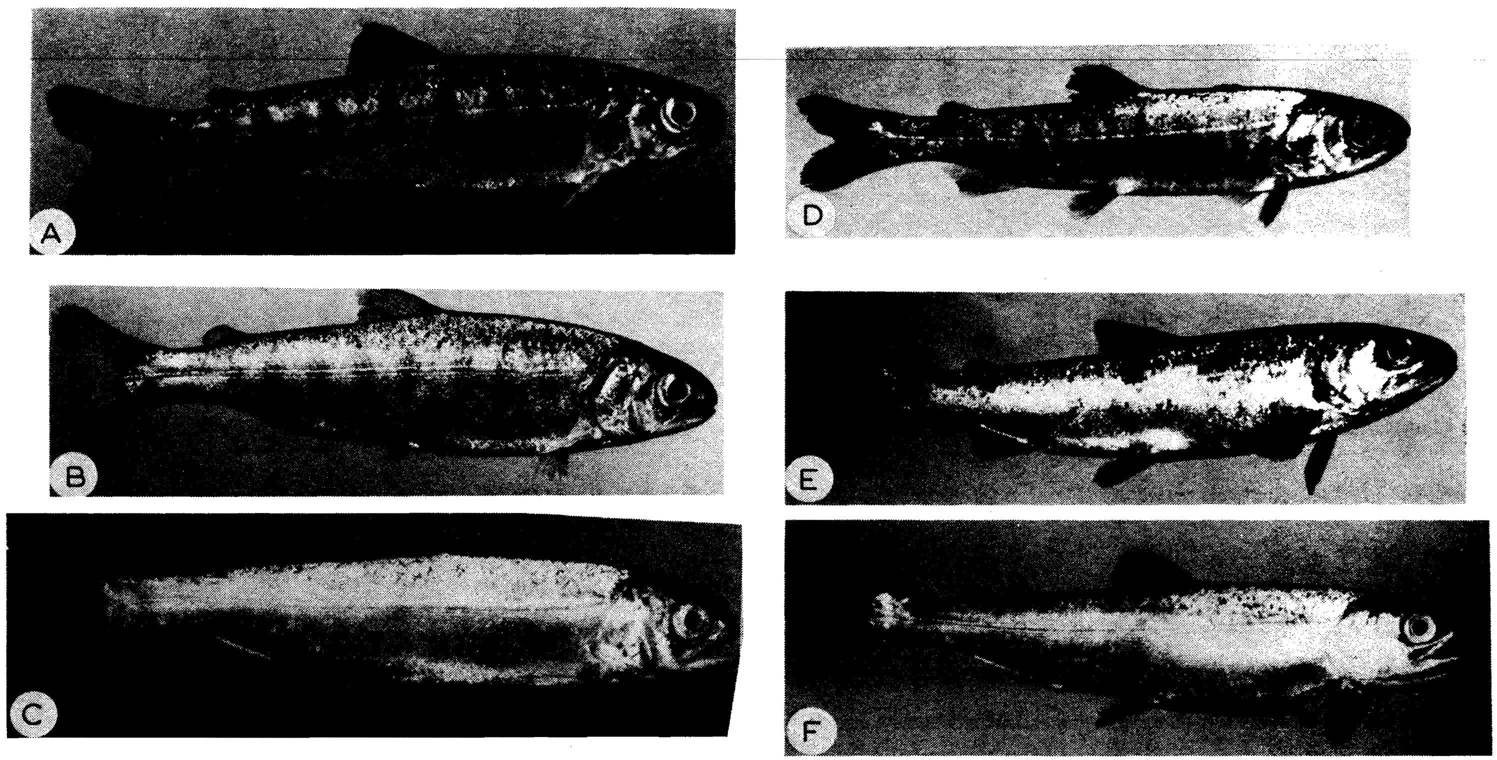


Fig. 2. Photographs of yearling coho salmon during the parr—smolt tranformation in fresh water (A—C) and after 4 months of residence in seawater (D—F). A, Parr; B, Transitional; C, Smolt No. 3; D, Seawater parr (revertant); E, Seawater transitional; F, Seawater smolt. See text for description of coloration.

The three groups of fish which were sampled from seawater on 18 August were selected by the following criteria:

*Seawater parr (revertant)*: parr marks faintly to boldly evident; fins yellow to orange-brown, often with a white margin on the anal fin; dorsal surface brown; ventral surface gray with a strongly mottled appearance; external sheen bronze or absent; and fish generally very thin and "pinheaded" (relatively microcephalic; Fig. 2D).

*Seawater transitional*: parr marks partially distinguishable, yellow pigment evident in fins, dorsal surface faded from metallic blue to green-brown, faintly speckled on ventral surface, and overall sheen no longer silver but golden to bronze. $E : L$ less than that of a parr (Fig. 2E).

*Seawater smolt*: externally the same as freshwater Smolt No. 3, dorsal surface now a bold metallic blue, and body form is again robust after a month or two of seawater residence (Fig. 2F).

The numbers of specimens taken from the larger group at each date are shown in Table I, along with their body lengths and scale measurements.

TABLE I

**Age, body length and scale measurements of yearling coho salmon at various stages of development. Fish from group A through E are parr through smolt stages sampled from fresh water. Groups P, T, and S are parr, transitional and smolt stages sampled from seawater net pens (SEM, standard error of the mean)**

| Specimen | Age (month) | Total body length (mm) | Scales | |
|---|---|---|---|---|
| | | | Circuli No. | *F—L* radius (μm) |
| Parr 1 | 16 | 105 | 24 | 496 |
| Parr 2 | 16 | 101 | 19 | 432 |
| Parr 3 | 16 | 109 | 15 | 403 |
| Parr 4 | 16 | 96 | 18 | 431 |
| Parr 5 | 16 | 105 | 23 | 568 |
| Parr 6 | 16 | 108 | 22 | 493 |
| Parr 7 | 16 | 101 | 17 | 419 |
| (Mean ± SEM) | | 104 ± 2 | 20 ± 1 | 463 ± 24 |
| Transitional 1 | 17 | 120 | 24 | 546 |
| Transitional 2 | 17 | 118 | 23 | 625 |
| Transitional 3 | 17 | 134 | 25 | 663 |
| Transitional 4 | 17 | 111 | 20 | 451 |
| Transitional 5 | 17 | 114 | 22 | 521 |
| Transitional 6 | 17 | 114 | 21 | 502 |
| Transitional 7 | 17 | 119 | 25 | 513 |
| (Mean ± SEM) | | 119 ± 3 | 23 ± 1 | 546 ± 30 |

TABLE I (*continued*)

| Specimen | Age (month) | Total body length (mm) | Scales | |
|---|---|---|---|---|
| | | | Circuli No. | *F—L* radius ($\mu$m) |
| Smolt No. 1,1 | 17.5 | 124 | 25 | 629 |
| Smolt No 1,2 | 17.5 | 120 | 27 | 612 |
| Smolt No. 1,3 | 17.5 | 119 | 17 | 449 |
| Smolt No. 1,4 | 17.5 | 118 | 17 | 436 |
| Smolt No. 1,5 | 17.5 | 112 | 26 | 623 |
| Smolt No. 1,6 | 17.5 | 121 | 17 | 485 |
| Smolt No. 1,7 | 17.5 | 118 | 23 | 367 |
| (Mean ± SEM) | | 119 ± 4 | 22 ± 2 | 514 ± 43 |
| Smolt No. 2,1 | 17.5 | 120 | 22 | 600 |
| Smolt No. 2,2 | 17.5 | 121 | 26 | 606 |
| Smolt No. 2,3 | 17.5 | 129 | 25 | 720 |
| Smolt No. 2,4 | 17.5 | 112 | 22 | 470 |
| Smolt No. 2,5 | 17.5 | 126 | 30 | 643 |
| (Mean ± SEM) | 17.5 | 122 ± 3 | 25 ± 2 | 608 ± 45 |
| Smolt No. 3,1 | 18.5 | 130 | 27 | 658 |
| Smolt No. 3,2 | 18.5 | 132 | 28 | 722 |
| Smolt No. 3,3 | 18.5 | 145 | 29 | 727 |
| Smolt No. 3,4 | 18.5 | 140 | 27 | 657 |
| Smolt No. 3,5 | 18.5 | 123 | 28 | 680 |
| Smolt No. 3,6 | 18.5 | 146 | 28 | 715 |
| (Mean ± SEM) | 18.5 | 136 ± 4 | 28 ± 1 | 693 ± 14 |
| SW P 1 | 21 | 119 | 22 | 527 |
| SW P 2 | 21 | 129 | 25 | 568 |
| SW P 3 | 21 | 125 | 31 | 645 |
| SW P 4 | 21 | 129 | 26 | 643 |
| SW P 5 | 21 | 130 | 28 | 682 |
| SW P 6 | 21 | 128 | 27 | 609 |
| (Mean ± SEM) | | 127 ± 2 | 27 ± 2 | 612 ± 25 |
| SW T 1 | 21 | 141 | 32 | 723 |
| SW T 2 | 21 | 135 | 35 | 807 |
| SW T 3 | 21 | 134 | 33 | 686 |
| SW T 4 | 21 | 137 | 28 | 682 |
| SW T 5 | 21 | 140 | 34 | 737 |
| SW T 6 | 21 | 132 | 31 | 653 |
| (Mean ± SEM) | | 137 ± 2 | 32 ± 1 | 715 ± 27 |
| SW S 1 | 21 | 156 | 35 | 900 |
| SW S 2 | 21 | 168 | 34 | 826 |
| SW S 3 | 21 | 158 | 34 | 773 |
| SW S 4 | 21 | 169 | 39 | 972 |
| SW S 5 | 21 | 158 | 38 | 846 |
| SW S 6 | 21 | 153 | 31 | 656 |
| (Mean ± SEM) | | 160 ± 3 | 35 ± 1 | 829 ± 49 |

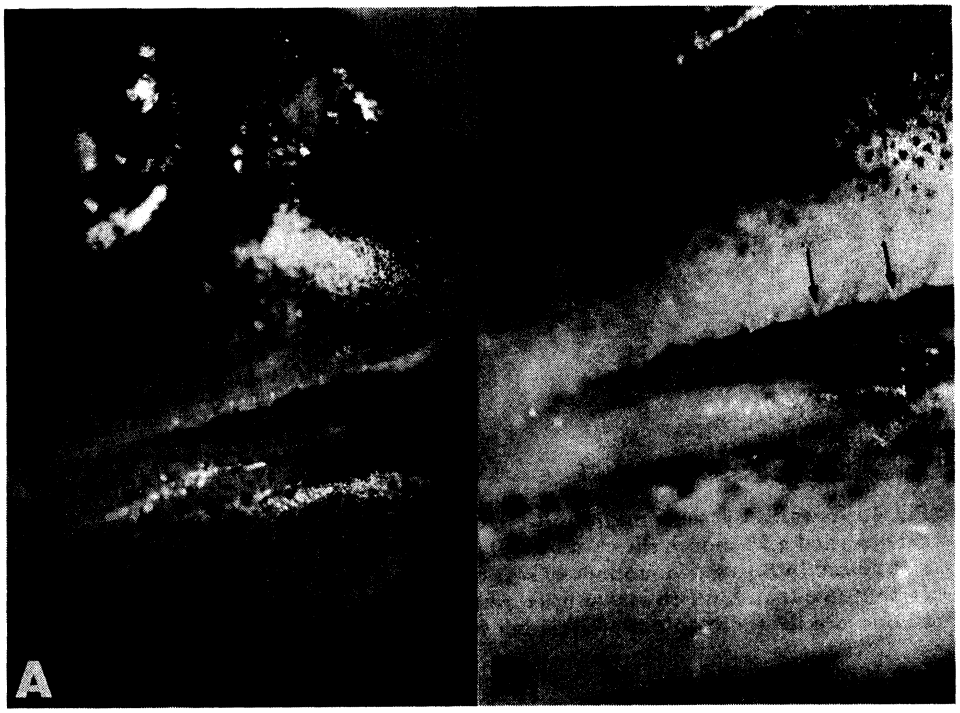


Fig. 3. Photographs, at the same magnification, of the jaws of a 16-month parr (A) and a 21-month seawater silvery smolt (B). In A no teeth have emerged from the "gum" tissue, the white tissue seen in profile within the two jaws. Within the gums some teeth can be seen as small refractive triangular structures. In B teeth have emerged from the gums. Arrows indicate two teeth that are in good focus. The places where they emerge from the gum are near the tips of the arrows. Thus, the actual lengths of the erupted teeth are greater than the profiles seen most clearly in the photograph.

All animals were preserved for longer term study in 5% formalin. Morphological study was oriented toward finding externally visible anatomical structures that change sufficiently during the parr—smolt period so that their separate developmental progress could be followed. It was felt features that change strikingly during this phase of development could be used as indices of progress in smoltification. Such study revealed that the following structures can serve such a purpose.

(a) *Teeth* on both jaws and on the tongue (Figs. 3 and 4).

(b) *Integumentary structures on both sides of the cloacal opening* (Fig. 5).

(c) *Integumentary structures lateral to the pelvic fins*, referred to in textbooks as "auxiliary appendages" (Fig. 6).

(d) *Scales* taken from an area dorsal to the lateral line.

(e) *Pigmentation*, both silvering on the body and melanic darkening of fins, including especially the dorsal and caudal fins. Progressive darkening of the edge of the septum that divides the choana (nostril) into two halves also is a

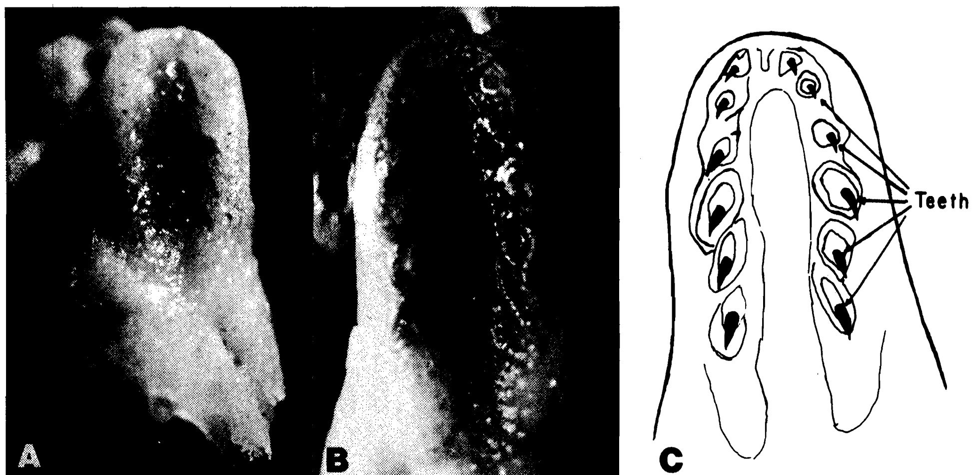


Fig. 4. Views, at the same magnification, of the dorsal sides of the tongues of a 16-month parr (A) and a 21-month silvery seawater smolt (B). In A no teeth have emerged from the soft tissue. In B rounded mounds of soft tissue surround long posteriorly pointing erupted teeth. C is a sketch which makes interpretation of the photograph, B, more easily understood since the teeth do not photograph well.

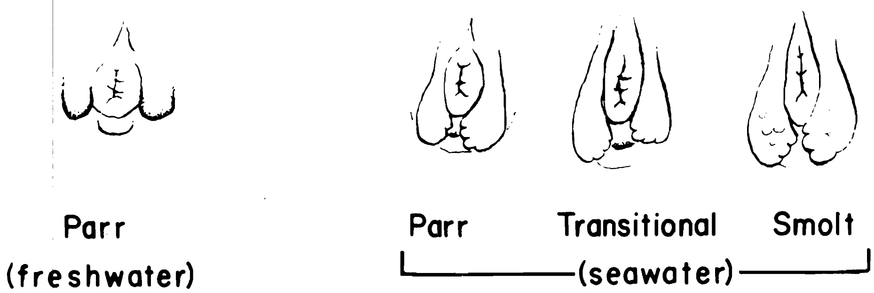


Fig. 5. Drawings, approximately to scale, of the cloacal openings of parr—smolt specimens of the indicated lengths. Anterior is up. In the freshwater parr, the cloacal terminus is rounded and it is flanked by two blunt rounded fleshy lobes. With age, the para-cloacal structures grow posteriorly and medially from an attached point to each side of the cloaca and the extensions are leaf-like and become lobulated at their ends. There is a medial swelling just posterior to the cloacal opening (shown for freshwater parr and seawater transitional) which in older animals may develop small finger-like posterior extensions or lobes. In the larger seawater smolt the surface of the para-cloacal folds themselves develop small scale-like leaflets. The seawater parr, though it is a "parr" with respect to pigmentation, is 7 months older than the parr in fresh water. It has relatively well-developed para-cloacal folds. All fish older than the 16-month-old parr develop a concavity (the edge of which is shown here as a thin arc-shaped line) into which the various other structures shown here are recessed, presumably for streamlining.

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Fig. 7. Photograph of a scale taken from a yearling smolt 110 cm long, showing the axis along which measurements were taken. $F$ is the point at which diametric axes cross. It is in the middle of the small round "nucleus", which is the first scale structure laid down in the young parr. $F$—$X$ is the antero-posterior radius which projects directly posterior. 17.5° to one side of the $F$—$X$ radius is the $F$—$L$ radius, which was followed in making successive measurements of the distances between circuli, the dark rings formed during progressive growth of the scale. Total distance $F$—$L$ and the total numbers of circuli also were recorded.

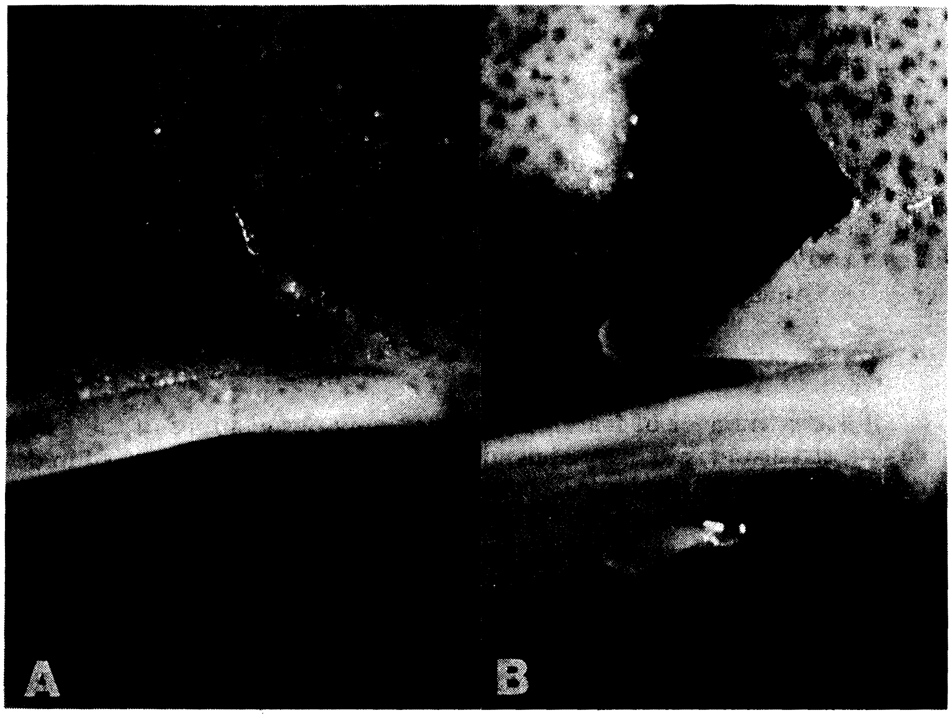


Fig. 6. Photographs of the auxiliary appendages of the pelvic fins of a 16-month parr (A) and a silvery seawater smolt (B) at the same magnification. A piece of black sheet plastic has been inserted between the auxiliary appendage and the body wall in each case. The bases of the pelvic fins are below. The appendage in A is rounded, knob-like and almost transparent. The appendage in B is longer and triangular instead of cylindrical in cross-section. In B a straight ventrolateral edge of the appendage is visible as well as structures on the surface of the organ.


Fig. 7.

fairly constant feature of smoltification. This requires examination under a dissecting microscope.

Scales were taken only from the area just above the lateral line, between the dorsal and adipose fins. They were mounted between two clear plastic layers and their images projected onto a screen which is part of a computerized device that yields digital data concerning the distances between successive circuli on the scale. In practice a probe is placed upon the image of each circulus and its position recorded from a reference point on the scale (the "focus"; Fig. 7). The separate measurements are recorded on a printout for each scale.

## RESULTS

Of a large number of features examined only observations of the teeth, cloacal structures, auxiliary appendages and scales will be discussed in detail below. The caudal fin shape has an interesting development from forked in parr—smolt to paddle-shaped in the adult (evidently more efficient for sustained swimming). However, the changes during the parr—smolt period are minimal. The otolith also has been used in establishing age and developmental history of salmonid fish (see Kim, 1963; Wilson and Larkin, 1980). However, it is often technically difficult to prepare otoliths so that daily growth rings over an extended period of time can be visualized. Furthermore, sampling of the otolith requires sacrifice and dissection of the fish. Nevertheless, analysis of otoliths may be of some use in establishing the age of individuals.

### *Teeth*

In 16-month coho parr, developing "normally" under hatchery conditions, teeth were very small. Although barely visible under a dissecting microscope because of their refractile properties and having not yet emerged from the gum, the teeth could be probed with a dissecting needle within the translucent gum-like tissues just inside the upper jaw (maxilla) and the lower jaw (mandible) (Fig. 3A). Similarly, on the dorsal surface of the tongue, teeth were felt by use of a probe. On the other hand, maxillary teeth projecting out of the gum tissue were visible even to the unaided eye in 22-month-old seawater smolt (Fig. 3B). Under the dissecting microscope teeth could be readily counted and measured. The lingual teeth of the 22-month-old coho were striking, especially in profile, being long and recurved, pointing in a posterior direction (Fig. 4).

These two conditions represent the extremes, and intermediate stages of dental growth were seen in animals of intermediate age and development. The 22-month-old seawater "parr" had rather well-developed teeth on the jaws and tongue and were far more advanced than the 16-month-old parr, though not quite as advanced as the silvery smolt of the same (22-month) age.

*Para-cloacal skin folds*

As shown in Fig. 5 there are progressive changes in integumentary folds that surround the cloacal opening. In the 16-month-old parr the cloacal termination itself is rounded and it is flanked on either side by two stubby rounded protuberances. With time, the cloacal opening becomes more elongated antero-posteriorly. The two lateral integumentary structures grow posteriorly and medially and thinner at the same time. During the elongation the medial posterior portion of this fold becomes lobulated. In the 22-month-old smolts the two folds almost meet in the midline, posterior to the cloacal aperture and, furthermore, their ventral surfaces develop secondary "sculptured" or scale-like structures. The area of the ventral body wall posterior to the cloacal aperture becomes hollowed out in a shallow bowl-shaped form to contain these integumentary folds in the older parr and smolt. In the 22-month-old seawater parr the cloacal opening is more rounded than in the silvery smolt of the same age, but the para-cloacal folds are well developed to a much greater extent than in parr at 16 months.

*Auxiliary appendages of the pelvic fins*

There is a small rounded fleshy lobe in 16-month-old parr lateral to and extending posteriorly to the attached base of each of the pelvic fins. In 22-month-old smolt this structure has elongated and become pointed at its posterior tip. From the initial short rounded almost cylindrical shape, it becomes wedge-shaped or prismatic in its cross section in the seawater smolt (Fig. 6). In adult salmonids this structure is not much more fully developed, though it is larger than in the smolt. Its function is obscure, though it is characteristic of all salmonids. In seawater parr and seawater transitional specimens the auxiliary appendage of the pelvic fin (as it is known in some textbooks) resembles that of the silvery smolt more than it resembles the structure of 16-month-old parr in fresh water.

*Scales and pigmentation*

Determination of the patterns of circuli, which accumulate as a fish scale grows, has long been a valuable tool for ichthyologists studying the life cycles of numerous species of fish. Such use of the scales has been made for many years in salmonids (Malloch, 1910). Koo (1955) has shown in *Oncorhynchus nerka* that measured distances between circuli can be plotted to show age and alternating seasonal periods of growth that are correlated with temperature and availability of food in fresh water (Fig. 8).

It was hoped that the scales would provide a cumulative history of the experiences of the young salmon in the various parr—smolt age groups in this study. Unfortunately, the plotted scale measurements taken from fish kept under hatchery conditions showed no clearly consistent patterns (Fig. 9).


Fig. 8. Photographs of scales of smolt stage sockeye salmon collected at the same site, at successive dates in 1949 by T. Koo. A, 79 mm long, 22 June; B, 90 mm long, 28 July; C, 105 mm long, 24 August; D, 101 mm long, 22 June. In these scales, collected under natural conditions note that in A and D a region of closely spaced circuli (an "annulus") occurs close to the outer edge of the scale, corresponding to the first winter experienced by these specimens. In B and C more widely spaced circuli appear outside of the annulus, and more circuli have been added and scale radius is increased. The scale in the figure is a 10-mm zone of the magnified (approximately 200×) image. From the doctoral thesis of Koo (1955), University of Washington.

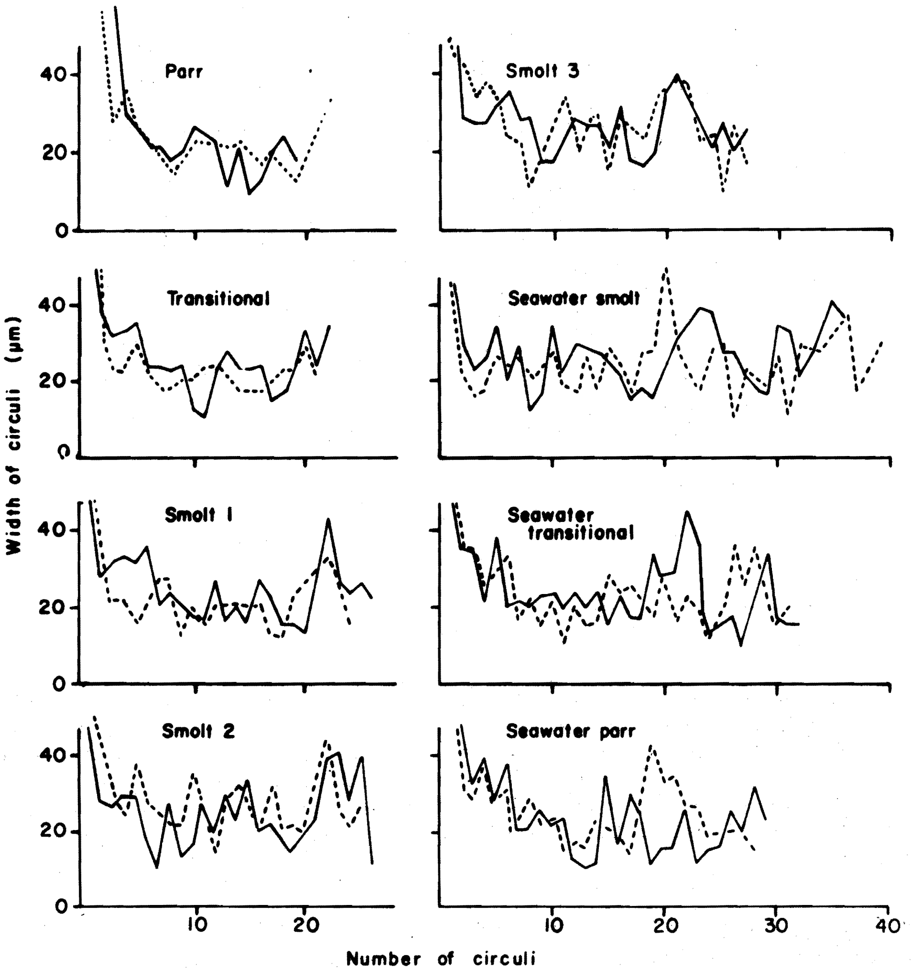


Fig. 9. The distances between successive circuli were measured along the *F*-axis and are plotted against the progressive numbers of the circuli outward from the focus. Each line (solid or dotted) represents measurements for one representative scale from an individual specimen taken from the various groups. Note that most of the scales from the smolt groups from freshwater and all of the groups from seawater have several particularly wide circuli between circuli numbers 18 and 28.

However, when two features of scale growth, the total number of circuli, and the *F—L* radius (Fig. 7) were plotted against age (Fig. 10) several interesting relationships were revealed. Body length increased as a regular arithmetic function of age between 16 and 22 months. If the mean measurements of the two scale parameters, total number of circuli, and the radius, were adjusted to the same amplitude as mean body length on the ordinate scale, they generally paralleled body length. However, an interesting deviation was observed between Smolt No. 1 and Smolt No. 2, which were separated from each other on the bases of developing body and fin color at the age of 17.5

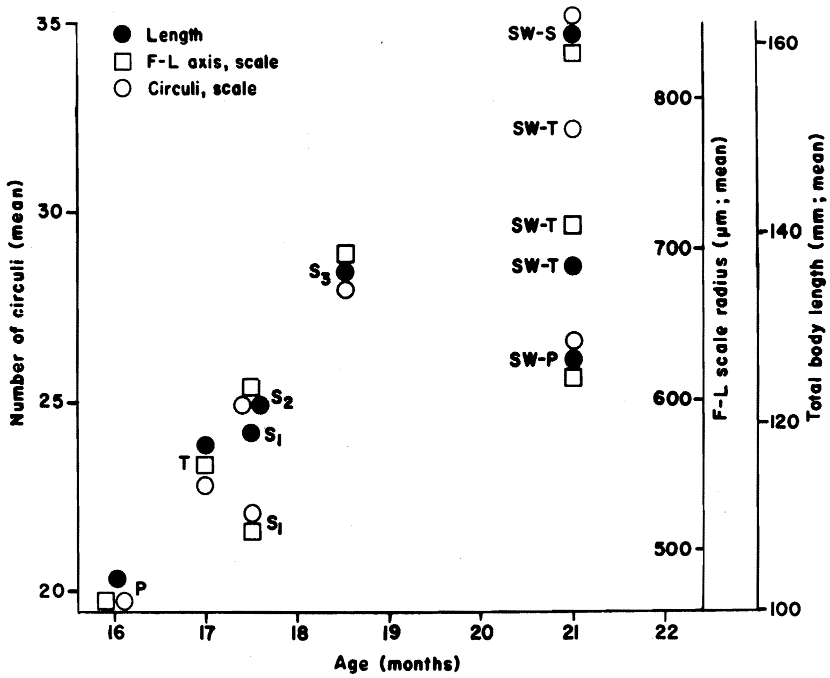


Fig. 10. Comparison of the averages of total body length, number of scale circuli, and scale radius of the nine groups of coho salmon. Note that in this graph the scale measurements of the smolt No. 1 group ($S_1$) are lower than the average body length for this group. On the other hand, scale measurements tended to be higher than body length of the transitional group in seawater (SW-T). In all other groups, all three parameters are closely grouped. P, parr; T, transitional; $S_2$, smolt No. 2, $S_3$, smolt No. 3; SW-P, seawater parr; SW-S, seawater smolt.

months. Smolt No. 2, in which silvering as well as melanic darkening of fin tips had begun, remained on the line of progressive "smoltification" with respect to the three parameters, body length, number of circuli, and *F—L* radius. However, in the Smolt No. 1 animals, although mean body length remained indistinguishable from Smolt No. 2, the two scale characters were differentiated.

Similarly, at 22 month of age differences were even more striking for seawater parr, transitional, and smolt. The parr-like specimens not only showed lower scale (circuli and *F—L* radius) measurements, but also they were much shorter than the silvery smolts. The incompletely silvered animals in the transitional group were intermediate between the seawater smolt and parr for both length and scale characteristics.

## DISCUSSION AND CONCLUSIONS

The development of all of the individual features that have been studied in parr and smolt coho salmon is gradual and continuous. This observation applies to body length, dentition, integumentary specializations next to the cloacal aperture and the pelvic fin, scale radius and numbers of scale circuli, and pigmentation. Even osmoregulatory ability in hypertonic media, which makes possible the most dramatic event in "smoltification", adaptation to the seawater environment, is itself not suddenly acquired (Conte and Wagner, 1965; Conte et al., 1966; Wagner et al., 1969; Kubo, 1970). Thus, use of the term metamorphosis to describe the parr—smolt period of development hardly seems justified.

In providing additional criteria to measure progress in parr—smolt development, this study has made possible several other generalizations. First, it has shown that differential rates in progress of some of the evolving features can occur even in normal uninterrupted development of coho salmon. Also, the slowing of development of scale structural features relative to growth in length (and in body weight) can occur in silvery smolt. For example, the average number of circuli and scale radius of Smolt No. 1 fish were lower than those of Smolt No. 2, while the averages of body length of these groups were similar (Fig. 10). More surprisingly, averaged scale measurements of Smolt No. 1 were less than those of the younger group of transitionals. This points out the heterogeneity of the parr—smolt development and is reminiscent of various morphological types of smolt and parr described by Kubo (1974, 1980). Inhomogeneity of developmental rates among individuals of a population of young salmon would appear to be a normal characteristic. As mentioned previously, genetically pre-determined desynchrony and variability of developmental rate can serve as an adaptive feature in salmonids. In these species an entire generation of breeding adult males and females is behaviorally simultaneously drawn back into its natal stream for reproduction. They are thus assembled within a limited time and in a restricted geographic site. Since salmon breed only once per lifetime, any profound disturbance, even of a temporary nature, in the spawning stream can eradicate an entire generation of salmon if it coincides with the breeding period. Heterogeneity of developmental rate and scattering of smoltifying animals over several years provide a mechanism for survival of at least part of a generation in such an event. Although this scattering is not a common natural occurrence in coho salmon in the southern part of their range, it is common in some salmonids and it is quite possible that the genetic potential for such an adaptive strategy is present in southern coho salmon. This genetic potential in coho salmon may be expressed in the heterogeneity of smoltification rate in a given population during a single season.

The phenotypic differentiation of coho smolts which appears in the seawater phase of development adds further to the heterogeneity of developmental rate and pattern. It is at this stage that the most obvious diversity in smoltification appears. For example, in the seawater specimens of the same age and the same exposure to seawater, there were wide ranges of difference of pigmentation, body length, and scale measurements. It is of interest that in comparing the extreme variants in seawater parr and smolt, dentition and integumentary characters (para-cloacal folds, auxiliary appendage of pelvic fin) were not strikingly different, even though there was considerable divergence in body length and scale measurements.

This illustrates the inaccuracy in defining the smolt stage on the basis of pigmentation alone. There would seem to be no difficulty in specifying the morphological features of a majority of normally developing coho smolts with the well-known pigmentary characteristics added to the several additional features described in this study. However, there seems to be no appropriate term to cover those animals which are advanced in development of some features but retarded or regressed in others. It would seem prudent in studies of the parr—smolt phase of salmonid development to avoid use of the terms parr and smolt except as general characterizations of a rather plastic organism. For more meaningful descriptions there seems to be no alternative but to include as many features as are known and can be measured or described. Thus, it is wrong to refer to a desilvered smolt as a parr, though it has lost its identifying silvery pigment; it may retain some melanic pigmentation on the fins and its scales, dentition and integumentary structures provide residual evidence that it has at one point reached a stage of development that characterizes the normal smolt. Although in this study we have referred to the individuals in the various sampled groups as parr, transitional, Smolt No. 1, No. 2, No. 3, etc., we are not proposing that this system be adopted as a nomenclatorial scheme. We have used these terms only for their operative utility. In a similar manner, "stunt" and "revertant" are useful as operational terms indicating in one instance a cessation of growth, and in the other a loss of a developed feature. However, even these names should not be considered definitive in precise usage, but should be accompanied by descriptions of as many other features as possible.

We are still at an early phase in the development of a more precise concept of the normal and experimentally altered patterns of development of young salmonids. A beginning has been made in this study in relating several more differentiating anatomical features to the process of smoltification in coho salmon. Additional experience with use of these features in studies by others under special circumstances, and with other stocks of salmon should greatly increase their value and significance. It is quite possible that more precise and detailed descriptions of developing salmonids will greatly clarify the properties of the developmental process in young salmon and trout, making possible its more efficient manipulation for man's benefit.

## ACKNOWLEDGEMENT

We would like to acknowledge the assistance of K. Myers and S. Sower during the course of this work which was supported by Washington Sea Grant (project RA-18) and National Science Foundation (PCM-7902695).

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