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THE SCALING AND POTENTIAL IMPORTANCE OF CUTANEOUS AND BRANCHIAL SURFACES IN RESPIRATORY GAS EXCHANGE IN YOUNG CHINOOK SALMON (*ONCORHYNCHUS TSHAWYTSCHA*)

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Summary

Measurements were made of the surface areas of the yolk sac, the fins, the head and trunk, the gill filaments and the gill lamellae of chinook salmon (*Oncorhynchus tshawytscha* Walbaum) weighing between 0.045 g (3.7 days posthatch) and 13.4 g (180 days posthatch). Cutaneous surfaces initially accounted for the vast majority (approx. 96%) of the total area available for respiratory gas exchange. As fish grew, total branchial surface area expanded at a more rapid rate than cutaneous surface area and, thus, came to represent a progressively larger fraction of total surface area. The transition was relatively slow, however, and it was not until fish reached 2.5–4.0 g that branchial area exceeded cutaneous area.

Although some individual surfaces (e.g. the gill lamellae) followed rather complex patterns of expansion, the overall increase in respiratory surface area with tissue mass could be described reasonably well using only two equations; one for the period prior to complete yolk absorption (<0.4 g) and one for the period following complete yolk absorption (>0.4 g). Mass exponents for total surface area (b=0.85) and metabolic rate (b≈0.8–0.9) were not significantly different for the larger fish. In contrast, the mass exponent for total surface area (b=0.39) was significantly less than that for metabolic rate (b≈0.9–1.0) for fish weighing less than 0.4 g. Changes in the relative efficiencies of the various exchange surfaces during the course of larval development probably account for this discrepancy.

Introduction

Studies of scaling in juvenile and adult fish have shown that gill surface area and aerobic capacity expand at roughly the same rate as fish grow (Muir and Hughes, 1969; Holeton, 1976; Hughes, 1979, 1984; Schmidt-Nielsen, 1984). This is usually interpreted as indicating that aerobic capacity is effectively limited by gill surface area. Recent ablation studies tend to support this hypothesis (Duthie and Hughes, 1987).

Key words: scaling, cutaneous surface area, gill area, metabolic rate, development, chinook salmon.

Relatively few studies have examined scaling during early life but what information is available suggests that gill area and aerobic capacity are not closely correlated in very young fish. In particular, the gill area of fish larvae appears to expand at a much more rapid rate in relation to body mass than does oxygen consumption. Allometric mass exponents for gill surface area typically seem to be in the range of 1.5–3.5 (De Silva, 1974; Hughes, 1981; Hughes and Al-Kadhomiy, 1988), although values as high as 7.1 have been reported (Oikawa and Itazawa, 1985). Mass exponents for metabolic rate, in contrast, are usually close to unity ($b \approx 1.0$; Giguere *et al.* 1988; Rombough, 1988*a*).

Hughes and Al-Kadhomiy (1988) recently suggested that the reason for the poor correlation between gill area and aerobic capacity in young fish is that other surfaces, in particular the skin, play a much more important role in gas exchange during early life than they do in older fish. They went on to speculate that, because of this, the appropriate indicator of larval exchange capacity is total surface area (gills+skin), not gill area. To date, no one has examined this hypothesis rigorously. Our goal, therefore, was to see if total surface area and aerobic capacity do, in fact, scale similarly in fish larvae.

We chose to use young chinook salmon (*Oncorhynchus tshawytscha*) as our model because we already had information for this species on how metabolic rate scales in relation to body mass during larval and postlarval development (Rombough, 1988*b*; Ure and Rombough, 1989). As a result, we were able to limit our experimental studies to an examination of the expansion of respiratory surfaces. The problem was to decide what surfaces were involved in larval gas exchange.

The few studies that have looked at the expansion of cutaneous as well as branchial surface area during larval development have, for the most part, restricted their examinations to the gill lamellae, the general body surface and the paired and unpaired fins. None of them has looked at the gill filaments or, at least explicitly, at the yolk sac. In young fish, filament area is initially much greater than lamellar area. For example, McDonald and McMahon (1977) reported that the filament area of arctic char (*Salvelinus alpinus*) 15 days after hatch is more than eight times the lamellar area. Thus, even assuming relatively inefficient transfer, a significant fraction of total branchial gas exchange probably takes place across the filaments. Similarly, the yolk sac initially accounts for a large fraction of cutaneous surface area. Liem (1981) showed that, at least in some species, the yolk sac acts as an extremely efficient countercurrent gas exchanger. Bearing all this in mind, we decided that a reasonable estimate of the effective surface area of young chinook could be obtained by including the surface areas of the gill filaments, the gill lamellae, the yolk sac, all paired and unpaired fins and the integument of the head and trunk.

Materials and methods

Gametes of chinook salmon were obtained from fish returning to spawn in the

Quinsam River, Vancouver Island, British Columbia, in October 1986 and again in October, 1987. In both years, eggs were pooled from two females and fertilized by the dry method with the pooled milt of four males. The resulting zygotes were reared in dechlorinated water from the City of Brandon domestic water supply (total hardness $\approx 240\,mg\,l^{-1}$). Prior to swim-up, the fish were raised in virtually total darkness. At swim-up, the fish were moved to a lighted environment and fed a mixed diet of commercial dry feed and beef liver. Temperatures after hatch averaged (±S.D.) 8.5±1.7°C and 10.2±2.4°C, respectively, in 1986/87 and 1987/88.

In 1986/87, fish were sampled at approximately evenly spaced intervals between hatch and swim-up (i.e. up to the start of exogenous feeding). In 1987/88, sampling was extended to include feeding alevins and young juveniles. Stage of development was recorded as accumulated thermal units from hatch (ATU= number of days posthatch×mean daily temperature). All specimens were fixed in 10% neutral buffered formalin (Humason, 1972). Tissue mass, that is the mass of the fish with the yolk removed, and standard length were determined following fixation. Specimens were then lightly stained with Grenacher's borax carmine (Humason, 1972) to facilitate handling and the measurement of surface areas.

Estimates of the surface areas of the yolk sac, the head and trunk, the fins, and the gill filaments and lamellae were made for a total of 49 fish ranging in size from 0.045 to 13.4 g wet mass. All area estimates were made by projecting magnified images of the various structures (using a Bausch & Lomb trisimplex microprojector) onto a digitizing tablet (Jandel Scientific model 2210). Projected images were calibrated using a stage micrometer (Bausch & Lomb) and analyzed using a computerized measurement system (Sigma Scan, Version 3, Jandel Scientific).

The surface area of the yolk sac was estimated by removing the integument from the surface of the yolk. The integument was cut into small pieces, each of which was approximately a flat surface. The pieces were placed on a glass slide and held in place with a coverslip. The image of the pieces was projected onto the digitizing tablet and the combined area of all pieces calculated. The surface area of the trunk, similarly, was estimated by removing the skin from the trunk, cutting it into small pieces and projecting the images onto the digitizing tablet. Estimates of the surface area of the head were made by projecting the image of the head onto the digitizing tablet and doubling the area measured (this procedure somewhat underestimates surface area since the head is not a flat surface). Estimates of fin area were made by projecting images of all paired and unpaired fins onto the digitizing tablet and doubling the measured area.

Estimates of filament surface area were made by removing all four gill arches from the right side of the fish. Gill arches were dissected into anterior and posterior hemibranchs and the number of filaments on each hemibranch was counted. Dissection of the hemibranchs involved dividing each arch into four segments and carefully plucking the filaments of the anterior hemibranch from the base of the arch. The plucked filaments and the intact segments of the posterior hemibranch were mounted in neutral buffered formalin on glass slides and

flattened by gently pressing on the coverslip. Care was taken to ensure that the filaments were not deformed. The projected images of all the filaments were traced on the digitizing tablet and their areas summed. The summed area was multiplied by four to take into account both surfaces of the filaments [we assumed, as did McDonald and McMahon (1977), that the filaments were flat plates] as well as the filaments on the left side of the body. Mean filament surface area was calculated by dividing the total filament area on the right side of the body by the number of filaments on that side.

Total lamellar surface area was estimated by multiplying mean lamellar surface area by twice the number of lamellae counted on all the filaments on the right side of the fish (lamellar counts were made in conjunction with the filament counts). Estimates of mean lamellar area were based on measurements of 36 representative lamellae from each fish. Representative lamellae were selected using a procedure similar to that recommended by Hughes (1984). This involved mounting 12 filaments, taken from the second right gill arch at approximately evenly spaced intervals along its length, in neutral buffered formalin on glass slides. The filaments were oriented so that the lamellae lay flat and the exposed areas of three lamellae, one each from the distal, middle and proximal portions of the filament, were measured. Bilateral area was taken to be twice the measured area.

Results

Analysis of covariance (Systat) confirmed that, with the exception of the yolk sac, there was no significant difference between the 1986/87 and the 1987/88 fish in terms of the scaling of the various body surfaces. The 1986/87 fish initially had slightly larger yolk sacs than an equivalent-sized fish obtained in 1987/88. However, since the yolk sac quickly became a minor fraction of total surface area we felt justified in combining the results from the two years.

Cutaneous surface area

Cutaneous surface area greatly exceeded branchial surface area in newly hatched alevins (Fig. 1). For example, at 3.7 days posthatch (37.4 ATU) the surface area of the skin was about 23 times that of the gills. The relative importance of the skin declined as development proceeded but cutaneous surfaces continued to represent in excess of 50 % of total surface area until the fish reached a mass of 2.5–4.0 g.

Initially the yolk sac was the largest component of cutaneous surface area, accounting for about 59 % of total cutaneous area at 37.4 ATU (Fig. 2). The importance of the yolk sac, however, decreased rapidly in both absolute and relative terms as yolk was consumed, and by the time the fish reached 0.4–0.5 g it was no longer present as a distinct structure. Conversely, the relative contributions of both the fins and the head and trunk increased during yolk absorption. Shortly after hatch (37.4 ATU), the fins and the head and trunk represented about 12 % and 29 %, respectively, of total cutaneous area. By the end of yolk absorption

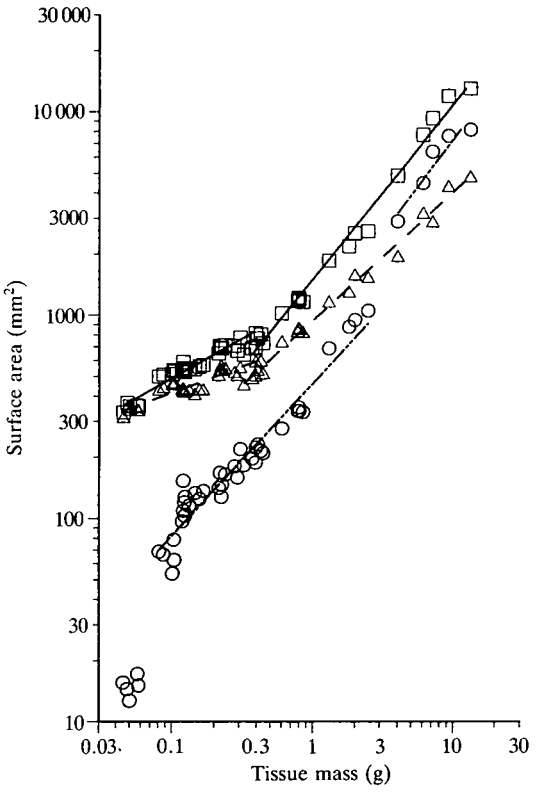

Fig. 1. Bilogarithmic plots showing the relative contributions of cutaneous and branchial surfaces to total respiratory surface area as functions of tissue mass in young chinook salmon. Equations describing the regressions are given in Table 1. △––, cutaneous surface area; ○– – –, branchial surface area; □——, total surface area.

(707 ATU), they respectively accounted for 36 % and 64 %. The rate of expansion of fins, however, was less than that of the head and trunk and, as a result, the relative contribution of the fins declined once the yolk was fully absorbed. By the time the fish reached 13.4 g (1838 ATU), the fins accounted for only about 25 % of total cutaneous surface area (the head and trunk accounted for the remaining 75 %).

Branchial surface area

At hatch, the gills accounted for only about 4 % of potential respiratory surface area. The gills, however, expanded rapidly during the early part of the alevin period so that by 103.5 ATU they represented about 13 % of total surface area (Fig. 1). Thereafter, their rate of expansion was slower but still more rapid than the rate at which cutaneous surfaces expanded. As a result, the gills came to constitute a progressively larger fraction of potential respiratory surface area. At 707 ATU (the end of yolk absorption), the gills accounted for about 28 % of total

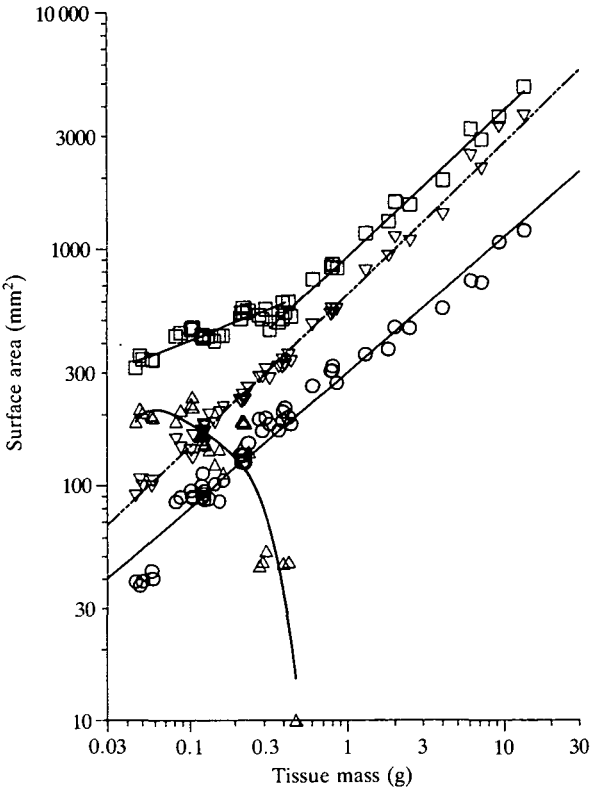

Fig. 2. Bilogarithmic plots showing the relationships between the area of various cutaneous surfaces and tissue mass in young chinook salmon. Equations describing the regressions are given in Table 1. △——, yolk sac area; ○——, fin area; ▽– – –, head and trunk area; □——, total cutaneous area.

surface area. By 1128 ATU (1.9 g), this had increased to 39 %. Gill area exceeded cutaneous area when the fish reached between 2.5 and 4.0 g (1128–1538 ATU). By the time the fish reached 13.4 g, branchial surface area was about 1.7 times cutaneous surface area.

Branchial gas exchange appears to be restricted initially to the gill filaments. Well-developed filaments were observed on both hemibranchs of all four gill arches at 37.4 ATU posthatch. Lamellae, in contrast, were present only as rudimentary structures, too small to measure using the current technique. The surface area of the filaments continued to expand at a more-or-less constant rate throughout the experimental period (Fig. 3). Lamellar expansion, in contrast, was discontinuous. There was a rapid proliferation in both the number and size of lamellae between 37.4 and 103.5 ATU. As a result, by 103.5 ATU the lamellae came to represent about 48 % of total branchial surface area. This proportion remained relatively constant until the fish reached about 2.5 g. Between 2.5 and 4.0 g there was a second period of rapid lamellar expansion, due primarily to a rather sharp increase in the size of individual lamellae. Mean lamellar area

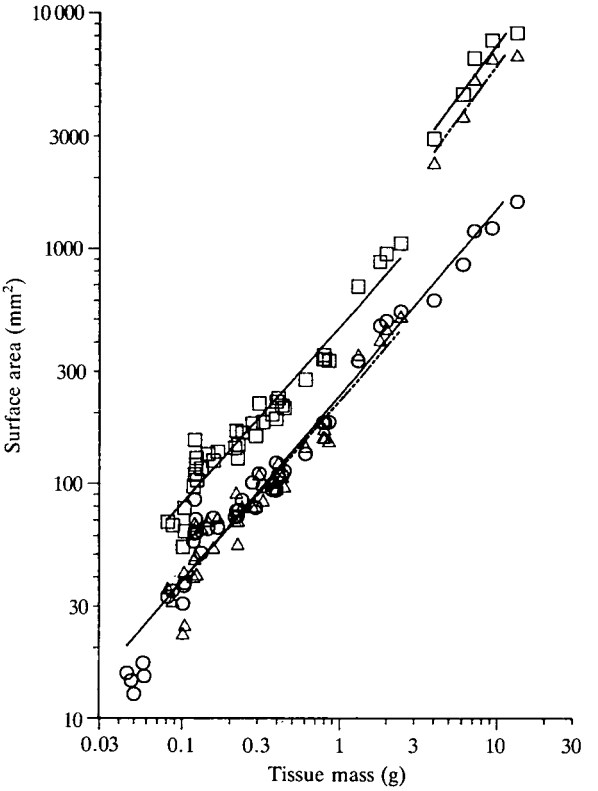

Fig. 3. Bilogarithmic plots showing the relationships between the area of various branchial surfaces and tissue mass in young chinook salmon. Equations describing the regressions are given in Table 1. ○——, filament area; △ – – –, lamellar area; □——, total branchial area.

increased from 7.8×10^{-3} mm^2 for a 2.5 g fish to 22.4×10^{-3} mm^2 for a 4.0 g fish. This rapid increase in mean lamellar area was reflected in an abrupt increase in the lamellar contributions to total gill area, from 48 % to 79 % of total gill area. The proportion of total gill area represented by the lamellae remained relatively constant, at about 80 %, in fish larger than 4.0 g.

Allometric relationships

The expansion of cutaneous surface area was best described by a biphasic relationship with mass exponents of 0.260 and 0.632, respectively, for the periods before and following complete yolk absorption (Table 1). The lower mass exponent prior to complete yolk absorption reflected the rapid decrease in the surface area of the yolk sac during this phase of growth (Fig. 2). Fin area and head and trunk area both expanded at more-or-less constant rates (mass exponents of 0.574 and 0.641, respectively) throughout the experimental period.

Compared with the skin, gill area followed a relatively complex pattern of

Table 1. *Allometric regressions* ($A=aM^b$) *relating the area* (A, mm^2) *of various body surfaces to tissue wet mass* (M, g)

Body surface (mm^2)	Range of body mass (g)	N	a	b (mean±S.E.)	r^2 (%)
Cutaneous surfaces					
Bilateral fin area	0.045–13.4	49	304	0.574±0.016	96.3
Head and trunk area	0.045–13.4	49	648	0.641±0.008	99.2
Total cutaneous area*	0.045–0.43	30	756	0.260±0.019	86.4
Total cutaneous area†	0.32–13.4	19	942	0.632±0.015	99.0
Branchial surfaces					
Filament area	0.045–13.4	49	237	0.792±0.023	96.1
Lamellar area	0.081–2.48	39	225	0.766±0.038	91.8
Lamellar area	4.01–13.4	5	713	0.922±0.189	88.7
Total gill area	0.081–2.48	39	463	0.750±0.032	93.7
Total gill area	4.01–13.4	5	918	0.900±0.171	90.2
Total surface area (cutaneous and branchial)					
Total area*	0.045–0.43	30	1202	0.390±0.019	94.0
Total area†	0.32–13.4	19	1501	0.857±0.020	99.0

* Indicates regressions based on data for fish prior to complete yolk absorption; † indicates regressions based on data for fish after complete yolk absorption.

expansion. As mentioned previously, filament area expanded at a constant rate ($b=0.792$) throughout the experimental period. Lamellar area, in contrast, showed four distinct phases of expansion (Fig. 3). Mass exponents were not calculated for the two brief periods of rapid lamellar expansion (37.4–103.5 ATU and 1128–1538 ATU) because of the relatively small change in mass that took place during these periods (0.052–0.095 g and 2.48–4.01 g, respectively). The mass exponents for the other two phases of growth (0.081–2.48 g and 4.01–13.4 g) were not significantly different (0.766 and 0.922, respectively). Since filament area expanded at a relatively constant rate, changes in the scaling of total gill area were determined in large part by changes in the rate of lamellar expansion. As for lamellar area, mass exponents were not estimated for total gill area during the periods between 37.4 and 103.5 ATU and between 1128 and 1538 ATU. Mass exponents for total gill area during the other two periods (0.081–2.48 g and 4.01–13.4 g) were slightly lower than those for lamellar area but, again, were not significantly different from each other (0.750 and 0.900, respectively).

In spite of the rather complex manner in which the gills expanded, we found to our surprise that the expansion of total surface area could be described adequately using only two equations; one for the period prior to complete yolk absorption ($b=0.390$) and one for the period following complete yolk absorption ($b=0.857$). It appears that, with the exception of the yolk sac, changes in the scaling of the various surfaces more-or-less compensate for one another to produce a relatively

constant rate of increase in total potential respiratory surface area within each phase of growth (Fig. 1).

Discussion

On the basis of mass exponents, total surface area appears to be an even poorer indicator of the exchange capacity of chinook larvae than does gill area. The metabolic mass exponent for chinook larvae is in the range of 0.9 (Ure and Rombough, 1989) to 1.0 (Rombough, 1988*b*). The mass exponent for branchial surface area is about 0.75 while that for total surface area is only about 0.4 (Table 1).

The poor correlation between total surface area and aerobic capacity is not particularly surprising given the diversity of the structures involved in larval gas exchange. Surface area is only one of the parameters that determine exchange capacity. Other parameters, particularly mean diffusion distance, the degree of perfusion and the extent to which the surface is ventilated, are also important. At any given stage of development, the various surfaces involved in larval gas exchange (i.e. the gill lamellae, the gill filaments, the yolk sac, the head and trunk and the various fins) differ significantly with respect to these parameters. Presumably, these differences are reflected in significant differences in the relative efficiencies of the various surfaces. To complicate matters further, these parameters change both qualitatively and quantitatively during the course of larval development. For example, in salmonids, mean lamellar diffusion distances decrease by almost 40 % as the alevins mature (Morgan, 1974). At the same time there is a corresponding increase in cutaneous diffusion distances as the body wall thickens and scales form. There are also changes in the pattern of blood flow (Balon, 1980) and the manner in which the various exchange surfaces are ventilated (Peterson, 1975). These changes, when combined with the changes in relative surface areas documented in this study, make it highly unlikely that a simple indicator such as total surface area will accurately reflect total exchange capacity throughout the course of larval development.

The situation is simpler in older fish in which the bulk of gas exchange (>80 % in juvenile chinook; Ure and Rombough, 1989) takes place across the gill lamellae and exchange parameters other than surface area remain relatively constant. Under such circumstances, one would expect the expansion of aerobic capacity to be closely linked to the expansion in lamellar area. This, in fact, has been demonstrated for a number of taxonomically diverse species (Muir and Hughes, 1969; Holeton, 1976; Hughes, 1979, 1984; Schmidt-Nielsen, 1984). It also appears to be the case for chinook once they reach about 4.0 g. Mass exponents for aerobic capacity ($b \approx 0.9$; Ure and Rombough, 1989) and lamellar area ($b = 0.92$; Table 1) are not significantly different for juvenile chinook weighing more than 4.0 g.

This study emphasizes the importance of the skin as a potential site of gas exchange in young chinook. At hatch, the skin accounts for about 96 % of the total area over which gas exchange can take place. The relative size of the skin

decreases as the fish grow but continues to account for more than 50 % of total surface area until the fish reach 2.5–4 g. Even in a 13.4 g juvenile, the skin still represents about 37 % of the total potential respiratory surface area. The efficiency of cutaneous gas exchange is probably less than that of the gills but, given its relatively large surface area, the skin undoubtedly accounts for a substantial portion of total oxygen uptake throughout larval development. Preliminary studies suggest that in excess of 80 % of total oxygen uptake takes place across the skin shortly after hatch (Ure and Rombough, 1989). The relative importance of the skin decreases as fish grow, but even in much larger fish than those used in this study the skin has been shown to account for a significant fraction of total oxygen uptake (approx. 15 % in a 286 g rainbow trout; Kirsch and Nonnette, 1977).

High rates of gill expansion shortly after hatch appear to be typical of teleost larvae. Most investigators have reported mass exponents in the range of 1.5–3.5 for gill area in young larvae (De Silva, 1974; Hughes, 1981; Hughes and Al-Kadhomiy, 1988). Oikawa and Itazawa (1985) indicated that the value may be as high as 7.1 in larval carp (*Cyprinus carpio*). We found that gill area also expanded rapidly in newly hatched chinook. Total gill area increased almost 4.5-fold between 37 and 104 ATU posthatch. During the same period, tissue mass increased by only about 80 %. This corresponds to a mass exponent for gill area of about 2.5. However, we do not feel it is particularly appropriate to describe gill expansion using mass exponents under such circumstances. In our opinion, allometric analysis is best suited to describe changes that take place over a relatively large size range (i.e. at least an order of magnitude). In this sense, some of the high mass exponents reported by other investigators are misleading. For example, the high rates of gill expansion reported by Oikawa and Itazawa (1985) and Hughes and Al-Kadhomiy (1988) for young larvae of carp and rainbow trout (*Salmo gairdneri*), respectively, were actually sustained for only relatively brief periods. In both species, tissue mass increased less than twofold during the period characterized by the high mass exponents. Since mass exponents are normally used to describe persistent rather than transitory trends, it may be more appropriate to consider the relatively brief but extremely rapid expansion in gill area that takes place shortly after hatch in terms of Balon's (1981) theory of saltatory development.

Chinook were somewhat unusual in that, unlike other species that have been examined so far, they displayed a second period of rapid gill expansion prior to assuming typical adult morphology. This expansion, occurring between 2.5 and 4.0 g, appears to be associated with the process of smoltification. Although we didn't test for salt water tolerance, the fish began to 'silver-up' (a visible indicator of smoltification) at about 4.0 g. This corresponds well with literature reports indicating that chinook are fully pre-adapted to sea water by the time they reach 5.0 g (Hoar, 1988). We did not examine the selective pressures behind the sharp increase in lamellar area during smoltification but several possibilities spring to mind. These include an increased demand for oxygen during the downstream

migration, greater osmoregulatory costs, at least initially, in sea water and a decrease in the availability of oxygen because of its lower solubility in sea water.

Note: Numerical summaries of the data presented graphically in this paper can be obtained by writing to the primary author.

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