

Changes in Midorbital to Hypural Length and Morphology in Maturing Sockeye Salmon

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Abstract.—The morphology of sockeye salmon *Oncorhynchus nerka* changes dramatically as the fish mature. The extent of those changes and whether or not midorbital to hypural length (MOHP) also undergoes change have not been examined. We measured MOHP, body depth, girth, and snout length of migrating sockeye salmon as they entered their natal lake, tagged them, and measured them again after recapture on the spawning grounds. All measured dimensions changed; MOHP decreased 5% in males, while body depth increased 18% and snout length increased 25%. Females changed less than males. Midorbital to hypural length did not change in a way that was explained by allocation of those resources into basal metabolism, secondary sexual development, or gonadal development. In order to use MOHP of mature adults to establish harvest rates on a small population within a fishing district, the change in MOHP should be established, as well as a conversion from the length measurement used at the time of fishing.

Sockeye salmon *Oncorhynchus nerka* undergo tremendous morphological change before spawning. During their homeward migration, before these changes are fully accomplished, sockeye salmon typically are subjected to commercial fisheries, during which length measurements from both the catch (captured fish) and escapement (fish migrating upriver past the fishery) are taken. Typically at this time, postorbital or midorbital to fork length is measured to exclude the rapidly changing snout length from the measurement. On the spawning grounds, subsequent to full maturation, length measurements may be taken again. At this point, because of wear of the caudal fin, postorbital or midorbital to hypural length is often the preferred measurement. The comparability of the two measurements from the midorbital has been examined at a fixed point in time for both the time of mi-

gration and at the time of spawning (Duncan 1956), but there has not been an examination of whether there are in fact changes in length associated with either of these measurements over the period between migration and spawning. Each set of measurements is used to compare the size of fish of different age-classes among years and locations. An understanding of the comparability of these measurements would enable managers to model probable harvest rates on individual spawning populations that make up larger stocks subjected to a common fishery.

Morphological development in maturing Pacific salmon generally results in an increase in snout development and, for males, an increase in body depth relative to length (Davidson 1935; Blair et al. 1993). Development of these secondary sexual traits can be both extreme and rapid (Davidson 1935). These physical changes may be quite costly energetically because migrating Pacific salmon cease feeding upon reentering freshwater and most of the morphological changes take place after freshwater entry (Hamon 1995). This means that the energy source for these changes is limited to resources gained during the ocean residence.

Because the fish cease feeding upon reentry into freshwater, length might be assumed to remain static. Alternatively, length might reflect resources potentially available for reallocation to secondary sexual characters, gametes, or basal metabolism. Reallocation would be suggested by a negative correlation between changes in length and changes in developing secondary sexual characters, changes in gametic investment, or total basal metabolism between reentry to freshwater and spawning. Any changes in length over this period would have important implications for comparisons of measurements obtained during the fishery and those obtained on the spawning grounds, both of which are commonly taken for management purposes.

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Our objective was to measure changes in secondary sexual characteristics and midorbital to hypural length in conjunction with maturation of sockeye salmon. Our approach was to take measurements on the same individuals at both freshwater entry and at sexual maturity, and analyze the changes in those individuals, in beach and stream spawning populations within a single lake.

Methods

Fish were captured with a beach seine as they entered Little Togiak Lake in the Wood River lake system of southwest Alaska between 4 and 14 July 1994. At this time, the morphology of the fish was not distinguishably different from what it was when they left the sea and passed through the fishery about 4 or 5 d earlier (Hamon 1995). Each fish received a numbered metal band around the dentary bone of the lower jaw. The linear distance from the midorbital to the hypural (MOHP) was measured, as was the length from the midorbital to the tip of the snout. Body depth and girth (at the anterior insertion of the dorsal fin perpendicular to the body's long axis) were also measured for each fish, after which they were released back into the lake. All measurements were recorded in millimeters. From 9 August to 9 September 1994, we recovered tagged mature fish on the spawning grounds within the lake by beach seine on the lake beaches and by dip net in the streams and repeated the previous measurements. In addition, we recorded the spawning condition of the females as ripe (distended bellies, expressing eggs) or spawned out (flat bellies, no eggs expressed).

Paired-sample *t*-tests were performed to examine whether the body dimensions of individual fish had changed. Regressions of MOHP on the changes in MOHP, body depth, snout length and girth were used to examine whether changes in length and development of secondary sexual characteristics varied with body size. Regressions of the change in MOHP on the changes in body depth, snout length, and girth were performed to determine whether resources initially reflected by MOHP were being reallocated to effect the changes in secondary sexual characteristics. Regression of the change in body depth and girth on the change in snout length was used to examine whether allocation was correlated in these traits. Body depth and girth were never tested against one another because these are essentially two different measures of the same dimension. To determine if time of spawning reflected variation in physical size of fish and if metabolic costs could

account for changes in length, we regressed the number of days from tagging to recovery (DTR) on both initial body length and the change in length. Sockeye salmon in Little Togiak Lake spawn along beaches and in small streams, and the fish spawning in streams are generally smaller and spawn earlier than fish spawning along beaches, so in cases where DTR was correlated with change in MOHP, analysis of covariance (ANCOVA) was used to determine if the effects were due to habitat differences. Finally, we compared the changes in MOHP of males to those of females using a two-sample *t*-test to investigate whether differences in length changes might be attributable to differences in gametic allocations because females use substantially more energy for gonad development than males (Wood and Foote 1996). Throughout, we use a probability decision of $P = 0.05$, and model I regressions.

Results

We tagged 837 fish as they entered the lake. We recovered 32 males and 27 females. The number of days from tagging to recovery (DTR) ranged from 21 to 64 d (mean, 46.77; SD, 12.09). Fish were captured from 10 spawning locations around the lake, four streams and six beaches.

Each measured dimension of males changed from the time of initial tagging to recovery. Midorbital to hypural length decreased, and snout length, body depth and girth increased (all $P < 0.0001$; Table 1; Figure 1). The relation between initial MOHP and the change in MOHP was not significant (both $P > 0.40$; Table 2). However, the relationships between the changes in snout length, body depth, and girth with initial MOHP were all significant (all $P \leq 0.01$; Table 2). The changes in body depth, snout length, and girth were not significantly related to the change in MOHP (all $P > 0.20$; Table 2). However, the change in body depth and the change in girth were positively correlated with the change in snout length (both $P \leq 0.0001$, Table 2). The relationship between DTR and MOHP was significant ($P < 0.001$), but that between DTR and the change in MOHP was not significant ($P > 0.25$).

Most measured dimensions of females also changed from the time of initial tagging to recovery. Length and girth decreased ($P < 0.0001$; $P < 0.05$; Table 1; Figure 1) while snout length increased ($P < 0.0001$; Table 1; Figure 1). Body depth did not change ($P > 0.10$; Table 1; Figure 1). The ripeness of the mature females strongly influenced the measured change in body depth and

TABLE 1.—Means (SDs) of measurements (millimeters) of immature and mature sockeye salmon in Little Togiak Lake. Statistical probabilities are indicated as $P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$, $P < 0.0001^{****}$.

Sex and measurement	Immature fish	Mature fish	Paired difference	<i>N</i>	Paired <i>t</i>
Male					
Body length	492.82 (41.39)	474.46 (41.95)	18.36 (9.73)	28	9.987****
Snout length	63.34 (10.02)	94.06 (15.97)	-30.72 (10.40)	32	-16.710****
Body depth	145.04 (19.91)	183.11 (32.98)	-38.07 (19.83)	28	-10.157****
Girth	358.56 (45.47)	421.76 (76.15)	-63.20 (39.57)	25	-7.986****
Female					
Body length	461.36 (39.62)	448.52 (36.44)	12.84 (9.89)	25	6.494****
Snout length	45.30 (6.33)	56.37 (9.09)	-11.07 (6.67)	27	-8.630****
Body depth	126.67 (11.99)	123.13 (15.58)	3.54 (8.76)	24	1.981
Girth	319.29 (29.01)	308.29 (35.37)	11.00 (22.4)	21	2.251*

girth ($P < 0.001$; $P < 0.0001$). Length was positively correlated with the change in length ($P < 0.05$; Table 2), as was the change in snout length ($P < 0.01$; Table 1), while the changes in body depth and girth were not (both $P > 0.10$). The relationships of the changes in body depth, snout length, and girth with the change in length were not significant, nor was the relationship of the changes in body depth and girth with the change in snout length (all $P > 0.40$; Table 1). Including the ripeness of the mature fish did not improve the

relation between change in length and change in body depth or girth. The relationship between DTR with both the length and the change in length was significant ($P < 0.05$; $P < 0.025$; Table 2). When habitat type was accounted for, the relationship of change in length and DTR was no longer significant ($P > 0.10$). Change in length was different ($P < 0.05$) between males (-18.4 mm) and females (-12.8 mm; $P < 0.05$). Changes in relative length were still greater on average for males, though not significantly so ($P < 0.10$).

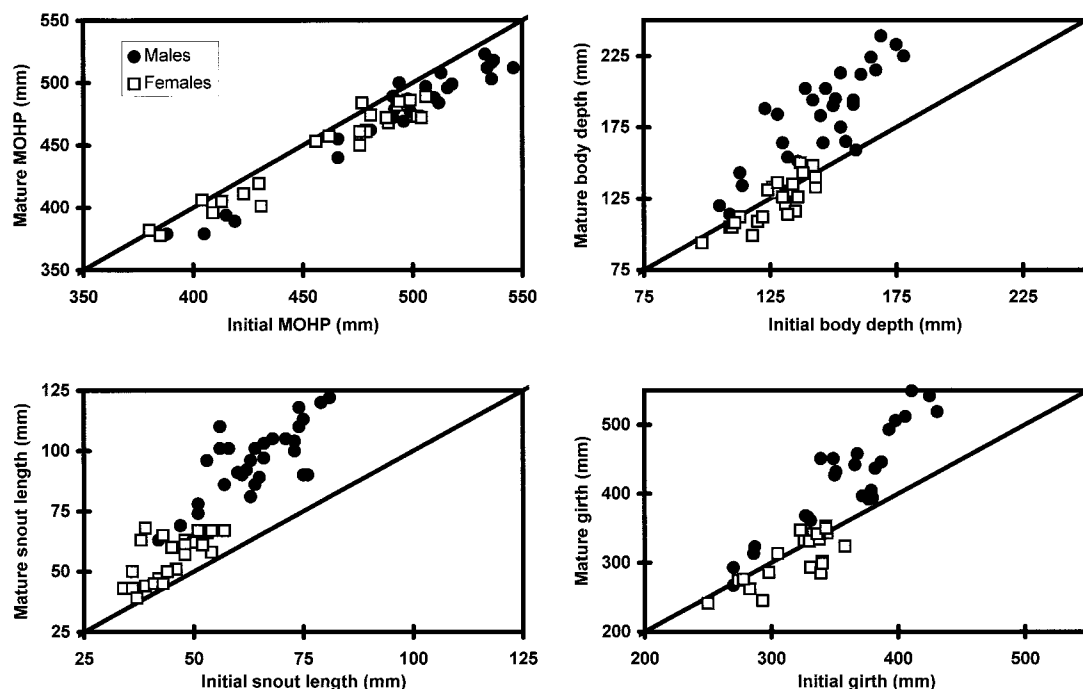


FIGURE 1. Scatterplots of body measurements (MOHP = midorbital to hypural length) taken at time of lake entry (initial measurements) and those same body measurements taken when the fish were mature, weeks to months later. Data points for males are represented by filled circles, those for females by open squares; the diagonal line represents the line of equality of initial and mature measurements.

TABLE 2.—Correlations among the changes (Δ) in body dimensions of maturing sockeye salmon and among those changes with overall body size and with the time spent in the lake, as measured by the number of days from tagging to recovery (DTR). Statistical probabilities are indicated as $P < 0.05^*$, $P < 0.01^{**}$, $P < 0.001^{***}$, and $P < 0.0001^{****}$.

Variable		Males			Females		
Independent	Dependent	<i>N</i>	Intercept (SE)	Slope (SE)	<i>N</i>	Intercept (SE)	Slope (SE)
Body length	Δ Body length	27	-11.464 (22.75)	0.014 (-0.05)	24	37.025 (21.71)	-0.108* (0.05)
	Δ Body depth	27	-78.306 (40.44)	0.236** (0.08)	22	-32.685 (20.62)	0.064 (0.04)
	Δ Girth	24	-204.839* (74.40)	0.545*** (0.15)	20	-25.076 (63.70)	0.030 (0.05)
	Δ Snout length	31	-39.546 (20.23)	0.143** (0.04)	26	-29.218* (12.19)	0.088** (0.03)
Δ Body length	Δ Body depth	27	25.515*** (7.80)	-0.684 (0.38)	22	-4.252 (3.04)	-0.101 (0.19)
	Δ Girth	24	37.497* (15.76)	-1.397 (0.75)	20	-6.615 (8.50)	0.345 (0.54)
	Δ Snout length	27	31.796*** (4.18)	0.021 (0.20)	24	10.702*** (2.19)	0.079 (0.14)
Δ Snout length	Δ Body depth	27	-5.255 (9.59)	1.346**** (0.29)	22	-2.986 (3.81)	0.006 (0.01)
DTR	Δ Girth	24	-20.758 (19.13)	2.657**** (0.58)	20	-3.530 (10.96)	-0.588 (0.77)
	Body length	32	409.680*** (23.95)	1.764*** (0.48)	26	395.693*** (30.22)	1.418* (0.65)
	Δ Body length	27	-10.721 (7.08)	-0.164 (0.15)	24	4.034 (6.96)	-0.379* (0.15)

Discussion

The midorbital to hypural length of males decreased by about 5%, while snout length increased 25%, body depth increased 18%, and girth increased 15%. Female length decreased slightly less than male length, and female snout length increased about 20%. The magnitude of morphological change in these animals over a brief period suggests a radical alteration in selection regimes on body shape. During the homeward migration, selection presumably favors a streamlined morphology for improved swimming efficiency (Taylor and McPhail 1985). The secondary sexual characteristics that develop after the end of the homeward migration may be the result of natural or sexual selection on the spawning grounds (Blair et al. 1993; Quinn and Foote 1994).

These results reinforce the importance of standardization of measurements between samples as to the maturity level of the individuals. Many dimensions of mature individuals are known to change over the course of development (Davidson 1935) and senescence (Quinn and Blair 1992). Body length measurements are used regularly in assessing size differences between catch and escapement in the fishery and between size at age at the different spawning grounds. Because the fish are not feeding, it may seem that the overall size

(body length) of the fish would not change. However, our results reinforce that measurements taken on length at the time of the fishery and on the spawning grounds are not comparable because fish length changes. Thus, any joint use of these two sets of measurements would need to account for both the differences in length measurements and the change in length that occurs between the measurements or provide a sensitivity analysis showing that the conclusions reached in the study would be unaffected by the change in length.

Midorbital to hypural length of sockeye salmon is variable within populations but may also be quite variable among different populations (Blair et al. 1993; Hamon 1995). Comparable data collected during the fishery and on the spawning grounds could be used to assess approximate harvest rates on individual populations of spawning salmon. The spawning ground size information would be used to characterize the populations. With corrections for both the change in length and the differences in length measurements, selectivity curves generated from fishery data could be applied to populations on the spawning grounds in a reverse selection model to indicate the probable selection differential and the harvest rate on individual populations. This would enable managers to identify populations more likely to be subjected

to a high rate of harvest and monitor them specifically.

The observed decrease in midorbital to hypural length of sockeye salmon during maturation could be due to reallocation of those resources into other morphological features, into basal metabolism, or into gametic production. However, none of these possibilities appear consistent with our data. Reallocation of resources from length to other morphological features or into basal metabolism should be reflected by correlations between the change in length and the change in other morphological features or time between measurements. In fact, for males, none of these correlations was significant, while for females, the correlation of change in length with time between measurements was significant but seemed merely an artifact of correlations between habitat type and the time between measurements (populations in streams were recaptured earlier due to their earlier spawning times, and fish in those populations are also smaller than those in beach populations). Thus, neither of these possible allocations of resources that would lead to a decrease in body length is substantiated by this evidence. Similarly, reallocation of length resources into gametic production should be reflected by a greater proportional loss of length among females than males, but the reverse was observed.

The strict relation of time to metabolic expenditure is not clear because fish could alter metabolism by changing their position in relation to the water temperatures in the lake. Berman and Quinn (1991) found that chinook salmon *O. tshawytscha* in the Yakima River drainage chose holding sites that afforded them lower metabolic expenditure until the arrival of spawning season. Fish in Little Togiak Lake have a similar opportunity because the lake stratifies and develops a thermocline in midsummer, with temperatures ranging from 4°C to 12°C (T. R. Hamon, personal observation), so they may in fact regulate their behavior for metabolic savings. A more detailed study tracking body temperatures of individual fish within the lake would be necessary to definitively rule out a metabolic expenditure of length resources.

In summary, maturing sockeye salmon change

dramatically in dimensions reflecting secondary sexual development as well as in midorbital to hypural length, and these changes need to be considered if data collected at different points of maturation are to be used in a complementary way.

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