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Postlarval Development and Diet of the Largescale Sucker, *Catostomus macrocheilus*, in Idaho[1]

CRAIG MACPHEE

IN young suckers a series of morphological, physiological, and behavioral changes occur after the absorption of the yolk sac. Such larval phenomena have been studied extensively in other species of fish. Balinsky (1948) defined 46 stages in the development of minnows from the unfertilized egg to the acquisition of scales and the completion of the lateral-line canal. Le Cren (1951) found that two straight logarithmic regression lines were

[1] Contribution of the Idaho Cooperative Wildlife Research Unit; College of Forestry, University of Idaho; the Idaho Fish and Game Department; the Wildlife Management Institute, and the U. S. Fish and Wildlife Service, Bureau of Sport Fisheries and Wildlife, cooperating.

needed to describe suitably the length-weight relationship of the yellow perch, *Perca flavescens* (Mitchill), one for larval fish 6 to 30 mm. in fork length and one for larger fish. Stewart (1926) described developmental characteristics of the postlarval white sucker, *Catostomus commersoni* (Lacépède), and related changes in the position of the mouth from terminal to inferior with changes in feeding behavior. In addition to describing and contrasting the development and diet in postlarval and early juvenile stages of the largescale sucker, *Catostomus macrocheilus* Girard, this paper integrates some of the concepts developed by Balinsky, Le Cren and Stewart within a single species.

Materials and Methods.—Between June 28 and September 9, 1957, ten samples of young suckers were collected near redds created on or about June 22 by numerous spawning adults. The redds were located in the North Fork of the Payette River, about halfway between Cascade Reservoir and Payette Lake, Idaho. Information on largescale sucker spawning habits and temperatures for this stream are given by Keating (1958).

The weights of the fish were measured by means of an analytical balance and fork lengths by projecting their images on a screen and correcting for magnification. The writer is indebted to Mr. Osborne E. Casey, Idaho Department of Fish and Game, for his assistance in making field collections and in weighing and measuring the fish used in this study.

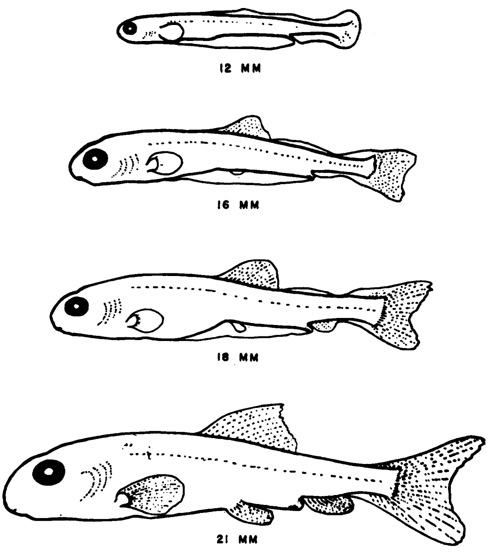

FIG. 1.—Four stages in the development of the largescale sucker, *Catostomus macrocheilus*.

Stomach contents of fish were counted in a Sedgewick-Rafter counting chamber. Total counts were made in most cases, but whenever a particular organism was abundant, totals were estimated by counting only a fraction of them.

Postlarval Development.—The morphology of postlarval fish has been investigated by many authors. Typically a median, pellucid fin fold (Fig. 1) is present which almost completely encircles the trunk and tail.

As indicated in Table I which lists the sequence of developmental events in postlarval and juvenile suckers, the anal-caudal, dorsal-caudal and pre-anal segments of the fin fold disappear in this order. The dorsal-caudal segment is present in largescale suckers about 18 mm. long. In contrast, Stewart (1926) stated that in white suckers, 9 mm. in length, the dorsal fin is well defined, the remainder of the dorsal median fin fold having disappeared.

In a specimen 8 mm. long the posterior vertebral column is quite straight and the caudal fin is diphycercal in shape. According to Norman (1947) such a tail is found in almost all larval or embryonic fishes. For a brief period, the caudal fin of the sucker is fundamentally heterocercal in that the caudal fin rays first appear ventral to the notochord, the tip of which turns dorsally with development. In suckers 15 mm. long, two hypural plates are outlined and the caudal fin is distinctly homocercal. As a result of differential growth, the rounded tail of early postlarvae changes to a double emarginate one before becoming forked. For the white sucker, Stewart (1926) reported that the two lobes of the caudal fin show at 12 mm. whereas they appear in largescale suckers about 14 mm. in average length.

Dorsal and anal fin lobes develop from thickened portions of the fin fold. An examination of the fin lobes in which rays were just developing indicated that the first few rays appear almost simultaneously, additional rays being added one at a time as the fish grows.

Quantitative relationships between the number of fin rays and body length are indicated in Fig. 2. Fish with no rays in the dorsal and anal fins are omitted from the graphs. Because the numbers of rays in the fins reach an upper limit, a curve of the type $R = A - Be^{-kL}$, which is asymptotic in character, was used to describe the distribution of points. A graphic method similar to that used by Brody (1945) was adopted for evaluating the constants. In this exponential equation,

TABLE I

DEVELOPMENTAL CHANGES IN THE POSTLARVAL LARGESCALE SUCKER, *Catostomus macrocheilus*

Structure	Number of specimens in transition range	Minimum length, mm.		Maximum length, mm.		Mid-point of transition range
		At which structure developed	At which structure dis-appeared	At which structure was not developed	At which structure dis-appeared	
Rounded tail	23		13.1		15.2	14.15
Double emarginate tail	35	13.1			15.2	14.15
Dorsal fin lobe	30	13.1		15.2		14.15
Forked tail	25	14.0		15.2		14.6
Dorsal fin rays	30	14.0		15.2		14.6
Pelvic fin buds	23	14.3		15.2		14.75
Anal fin lobe	23	14.3		15.2		14.8
Straight gut	24		14.6		16.0	15.3
Anal fin rays	33	14.3		16.5		15.4
Anal-caudal fin fold	21		15.1		17.3	16.2
Pelvic fin rays	12	16.0		17.4		16.7
Dorsal-caudal fin fold	27		16.0		19.5	17.75
S-shaped gut	26	14.6			23.5	19.05
Pre-anal fin fold	6		19.1		20.7	19.9
Coiled gut	3	23.2		23.5		23.35

R equals the number of fin rays; *A* represents the maximum number of rays possible; and *B* is a frequency parameter denoting an artificial value for the number of fin rays present when the size of the fish is extrapolated to zero length. The letter *k* stands for the instantaneous relative increase in length with respect to the maximum increase in rays to be made and the size class of developing fish is indicated by the letter *L*. The formula of the curve for the dorsal fin (76 fish) is $R = 13.3 - 4440e^{-0.446L}$ and that for the anal fin (57 fish) is $R = 8.8 - 108e^{-0.204L}$. A comparison of the two curves show that the number of rays commence to increase at an accelerated rate in the dorsal fins in contrast to those in the anal fins, the value of the asymptote for the dorsal being greater than that for the anal fin.

Of the paired appendages, the pectoral fins were already well developed in a postlarval sucker 8 mm. long. Pelvic fin buds begin to appear on white suckers, 15 mm. long, and on largescale suckers of about the same size.

In fish up to about 13 mm. long, in anterior view, the mouth has an inverted U-shaped outline, the tip of the jaws being about level with the middle of the eyes. As the fish grows, the jaws rotate from an inclined plane to a horizontal one so that the forward edge of the lower jaw which initially was almost below, eventually lies posterior to that of the upper jaw, the lower jaw lying within the curvature of the upper one. In fish 13 to 16 mm. long, the lower lip gradually changes from an inferior to a posterior position with reference to that of the upper lip. Thus, the upper lip remains in a terminal position longer than that of the lower one and in fish up to about 16 mm. in length the mouth might morphologically still be

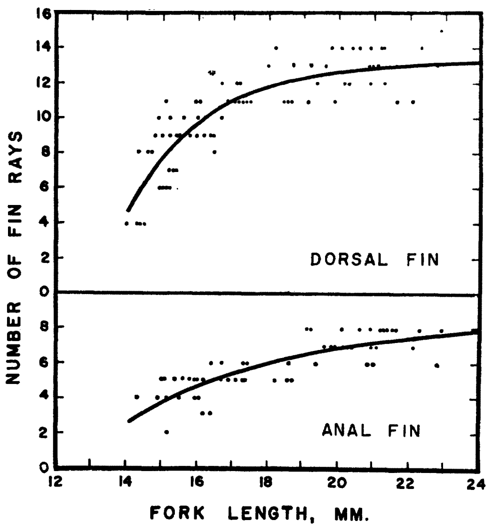

FIG. 2.—The relationship between body length and number of fin rays in the postlarval development of the largescale sucker, *Catostomus macrocheilus*.

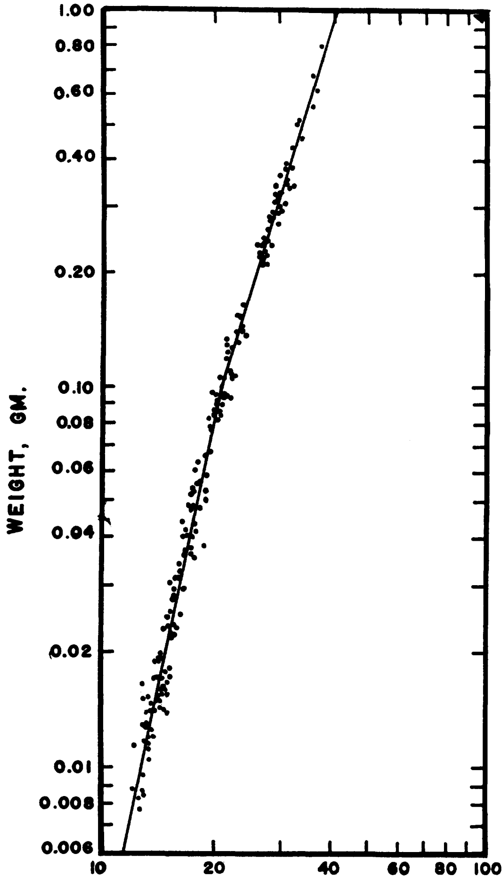

FIG. 3.—The length-weight relationship of 189 postlarval and juvenile largescale suckers, *Catostomus macrocheilus.*

TABLE II

COMPARISON OF THE PERCENTAGE OCCURRENCE OF VARIOUS FOOD ITEMS IN THREE LENGTH CLASSES OF THE LARGESCALE SUCKER

Catostomus macrocheilus

Food item	Fork length, in mm.		
	12.0–15.9 (55)*	16.0–23.5 (57)	23.6–38.0 (42)
Diatoms	29	60	90
Filamentous alga	0	0	10
Protozoans	13	35	69
Rotifers	71	82	69
Cladocerans	65	73	60
Midges	18	32	19
No Organisms	13	0	0
Detritus	0	0	17
Sand	0	2	26

* The number of specimens is given in parentheses.

considered terminal although functionally inferior in position. By the time the young sucker is about 19 mm. long, the upper jaw has migrated below the level of the lower margin of the eyes and is definitely inferior in position.

Length-Weight Relationship.—In most fishes where length-weight relationships have been studied, the postlarval stage of development has been omitted. In Fig. 3, a logarithmic graph illustrates the length-weight relationship of 189 young suckers. The relationship cannot be described adequately by a single straight line, for an inspection of the graph reveals that when the young fish attain a length of about 20 mm., a point of inflection occurs due to a change in growth rate. The formula, $\log W = (7.48295 - 10) + 4.9125 \log L$, describes the regression line of 113 suckers 12 to 20 mm. long, and the formula, $\log W = (7.95531 - 10) + 3.3496 \log L$, describes that of 76 suckers 20 to 38 mm. long. Fish smaller than 20 mm. increase in weight at a faster rate than those larger than 20 mm. in length.

The point of inflection is significant in that it marks not only the position of change in the growth form but also the end of all major physiognomic changes that have taken place during metamorphosis. For these two reasons, the point of inflection as determined by the point of intersection of the two regression lines can be used, at least in this species, as a relatively precise indicator of the upper limit of the postlarval stage of development.

Diet.—In order to analyze dietary change in postlarval and juvenile suckers, three length classes (Table II) which corresponded to three phases in the development of the digestive tract were chosen; namely, from a straight tube through an S-shaped state to a coiled tube. Both postlarval and juvenile fish are represented in the intermediate class.

All food items were counted in the straight digestive tract which was about 50 percent of the length of the fish. For the two larger length classes, the posterior limit of the stomach was arbitrarily delineated by severing the tract at the middle of the first reverse bend. The relative length of the gut examined was about 25 percent of the fork length for suckers 16 to 21 mm. and 29 percent for suckers 25 mm. long.

Only seven out of 154 suckers had empty digestive tracts. Because of their small size (12.9 to 15.3 mm.), they are associated with the "top-feeding" period described by Stewart (1926) in which the postlarval white sucker commenced to feed. The arithmetic mean and standard error of the relative condition coefficient (Le Cren, 1951) for these seven non-feeding fish were 0.90 ± 0.06 which indicates that although these non-feeding fish were thinner than the feeding ones they were not significantly so for the small sample tested.

An inspection of Table II reveals that the percentage occurrence of diatoms and protozoans increased progressively as the gut developed from a straight tube to a coiled one. The percentage occurrence of rotifers, cladocerans and midges, however, was greatest in the intermediate length class. A comparison of these data with those presented by Carl (1936) for immature largescale suckers from Shuswap Lake and largescale suckers from Eagle River, British Columbia, reveals several marked differences. In fish from Shuswap Lake, the percentage occurrence of cladocerans and midge larvae was greater than, and that of diatoms, far smaller than that found for fish from Payette River. In fish from Eagle River, no cladocerans were reported. In the Payette fish, neither ostrocods, copepods, stone fly larvae, water mites, nor terrestrial insects were found. In contrast, protozoans and especially rotifers were common. The numbers of midge larvae found in any one sucker were relatively few and consequently little significance can be attached to changes in their relative occurrence. Such qualitative differences in diet could reflect seasonal, geographical, and environmental variations in the species composition of available food organisms.

Sand grains were present in one fry, 22.4 mm. in length. In the largest length class, 11 fry, 26.7 mm. in average length, also contained sand grains and seven fry, 31.5 mm. in average length, contained detritus. The presence of sand and detritus in the stomachs of the fry suggests a change from a discriminate to an indiscriminate type of feeding behavior. It is noteworthy that such indiscriminate feeding followed the development of the coiled digestive tract, the added length of which is possibly better adapted for assimilating detritus.

In 154 fish, seven, one and five suckers in the shortest, intermediate and longest length classes contained an average of 13,000, 22,000, and 16,000 diatoms, the next highest count for one fish in each class being 127, 2,550, and 4,010 diatoms respectively. One 36 mm. sucker had eaten about 420 rotifers and 490 cladocerans. Such values marked the extreme tail ends of frequency distributions which were "Poisson-like" in shape because most fish ate little or none of any one particular food type and relatively few fish ate a lot of a single species of organism.

A comparison of the average number of food items for the 14 fish which ate the most extreme quantities of diatoms and invertebrates detailed above with the average per fish in Table III indicates that, in general, the majority of young suckers ate small quan-

TABLE III

A COMPARISON OF THE AVERAGE NUMBERS OF FOOD ITEMS EATEN PER FISH AND PER GRAM WEIGHT OF FISH IN THREE LENGTH CLASSES OF LARGESCALE SUCKERS, *Catostomus macrocheilus*

Food item	Size range, mm.	Number of fish	Average number of items per fish	Average weight of fish, gm.	Average number of items per gram weight of fish
Diatoms	12.0–15.9	48	8.6	0.017	506
	16.0–23.5	56	246	0.086	2860
	23.6–38.0	37	573	0.330	1740
Protozoans	12.0–15.9	55	0.3	0.018	17
	16.0–23.5	57	3.7	0.085	44
	23.6–38.0	42	17.2	0.334	51
Rotifers	12.0–15.9	55	25.7	0.018	1430
	16.0–23.5	57	25.5	0.085	300
	23.6–38.0	41	22.2	0.325	68
Cladocerans	12.0–15.9	55	4.9	0.018	272
	16.0–23.5	57	11.7	0.085	138
	23.6–38.0	41	11.5	0.325	35

tities of food. The 14 fish are omitted from the table since the inclusion of these few would distort the average of the majority. Fish in the smallest length class ate a relatively low proportion of diatoms and protozoans and a high proportion of rotifers and cladocerans, especially on a per weight basis. Differences in size of the digestive tube sampled make absolute comparisons of stomach contents difficult and such variations should be borne in mind when interpreting the data.

The "top-feeding" behavior of fish in the smallest length class accounts for the high utilization of cladocerans as well as the low utilization of diatoms and protozoans in the diet. About 18 per cent of the fish under 16.0 mm. contained cladocerans (*Bosmina* sp.) with clear, thin carapaces typical of pelagic forms. Their presence helps to substantiate field observations in which young suckers were observed near the surface of the water presumably feeding. Many suckers in this smallest class had eaten diatoms, bottom-dwelling protozoans and cladocerans with the dark, thick carapaces associated with bottom forms. This indicates that at least some of this group were already feeding on or near the bottom.

Discussion.—Although many phases in the development and food habits of the largescale sucker rather closely parallel those of the white sucker, *Catostomus commersoni*, the extension of knowledge to other localities and to other species is important in order to form certain generalizations for suckers as a whole. Such details of postlarval development as eye size, position and shape of intestine, C-shaped caudal fin and characteristics of the median fin fold are shown in a photograph of a humpback sucker by Douglas (1952). A comparison of this photograph with the smallest of the largescale suckers in Fig. 1 shows no marked morphological differences. Minor differences in development between the white sucker and the coarsescale sucker have already been mentioned. That an even closer resemblance exists among larvae than among adults of different sucker species, emphasizes the closeness of the phylogeny of the sucker family.

The white sucker described by Stewart (1926) is more developed for its size than the largescale sucker. This statement is substantiated by the early disappearance of the dorsal median fin fold, and the early definition of the dorsal fin and lobed tail.

Except for one individual 8 mm. in length, all suckers collected were 12 mm. or larger and had reached at least Stage 35 in the developmental scale outlined by Balinsky (1948). Stage 35 is characterized by having 7 to 9 caudal rays, the fin fold deepening at the sites of the future dorsal and anal fin rays, and the posterior end of the notochord bent upward. Based on major physiognomic characteristics, Stage 43, characterized by the complete absence of the median fin fold, represents the beginning of the juvenile stage and Stage 42, which still contains a posterior remnant of the pre-anal fin fold, represents the last of the postlarval stages of development. This contrasts with the suggestion of Winn and Miller (1954) that for minnows and suckers in general, the postlarval or feeding larva period should be considered to terminate at Stage 40. On the other hand, Le Cren differentiated between larval and juvenile perch by means of length-weight regression lines but did not indicate whether or not their point of intersection coincided with the termination of larval metamorphosis. In the largescale sucker, the point of intersection of the postlarval and juvenile regression lines at the 20 mm. point serves to separate Stage 42 and 43 as well as to mark a point of divergence in body form.

Not only must young suckers respond to food but they must also adapt their feeding behavior to correspond with modifications in body structures. Because these modifications are most pronounced in early life, any correlations which might exist between state of development and feeding habits are likely to be most marked in postlarval fish.

While the change in behavior pattern from a "top feeding" to a "bottom feeding" one is abrupt, yet morphological adaptations are necessarily gradual. This alteration in behavior is more closely associated with the posterior shift of the lower jaw, while the upper lip is still terminal, than with the migration of both jaws from a terminal to an inferior position. Stomach analysis show that this shift in the lower jaw does not prevent the postlarval sucker from selecting particulate food items such as cladocerans. Adaptation of the jaws for ventral feeding, however, does precede the lengthening of the digestive tract. Although a general rise in diatom consumption was associated with a change in position of the jaws and an increase in length of the intestine, indiscriminate feeding on detritus was not associated with the position of the jaws but rather, with the development of the coiled intestine.

Summary and Conclusions.—Except for

the coiling of the intestine in the largescale sucker, *Catostomus macrocheilus*, larval metamorphosis is complete in postlarvae about 20 mm. in fork length.

The length-weight relationships of postlarval and juvenile suckers are described by two straight logarithmic regression lines. The intersection of these lines coincides with the end of major changes in physiognomy and thus, could be useful as a criterion for designating the end of postlarval development.

Percentage frequency of occurrence for diatoms and protozoans was significantly higher in juvenile than in postlarval fish while that for rotifers and cladocerans was relatively uniform.

In general, the average number of diatoms and protozoans ingested per gram weight of fish was greater for juvenile than for postlarval suckers whereas the average number of rotifers and cladocerans eaten was considerably less for juvenile than for postlarval suckers.

A change in behavior from surface to bottom feeding is associated with a shift in the lower jaw of the mouth, whereas a behavioral change from discriminate to non-discriminate feeding is associated with the development of the coiled intestine.

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On the Swim Bladder and its Posterior Communication with the Exterior in an Indian Clupeoid Fish, *Ilisha indica*

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The swim bladder of certain clupeoids has been reported to possess in addition to the pneumatic duct an opening to the exterior at the posterior end, near the anus. This opening is thought by some to be a safety valve, but in fact little is known of its structure or function.

During the course of investigations on the swim bladder of teleostean fishes, the swim bladders of clupeoid genera commonly found in India (*Sardinella, Thrissocles, Ilisha* and *Pellona*) were observed to possess a well-developed posterior mechanism communicating with the exterior. The present paper is an attempt to elucidate the aspects of this complex modification in *Ilisha indica* (Swainson).

Historical Resumé

Weber (1820) described a communication with the exterior from the posterior end of the swim bladder of *Clupea harengus* through a duct opening into the genital pore between the genital duct and the ureter aperture. Huxley (1881) confirmed the presence of the posterior communication of the swim bladder of *C. harengus* with the exterior. Ridewood (1892) described the presence of this peculiar modification in the swim bladders of *C. harengus, C.* [= *Sardina*] *pilchardus, C.* [= *Alosa*] *alosa* and *Engraulis enchrasicholus*. Later, de Beaufort (1909) mentioned a direct communication of the swim bladder to the exterior through an aperture situated close