

Development, growth, and food of early life stages of Northern Pike (*Esox lucius*) and Muskellunge (*Esox masquinongy*) in the Upper St. Lawrence River



A typical spawning marsh of Northern Pike, this one is Flynn Bay in the St. Lawrence River.

John E. Cooper
Cooper Environmental Research
1444 County Route 23
Constantia, New York 13044
www.cooperenvironmentalresearch.com
2016

Abstract

Abstract.—Development and growth of eggs and larvae under varying regimes of temperature and diet were examined to test the hypotheses that Northern Pike larvae grow faster than Muskellunge larvae, that adhesive papillae were present only in Northern Pike larvae, and that Northern Pike eggs and larvae were more tolerant of cold water than were Muskellunge eggs and larvae. Eggs of both species were adhesive until water hardening. Larvae of both species possessed adhesive papillae, but Muskellunge used their papillae for less time than did Northern Pike. Northern Pike larvae attained various developmental characters at an earlier age than did Muskellunge in controlled and varying water temperatures. Growth of most body structures was similar but snout length was greater in Muskellunge larvae. Northern Pike larvae grew faster than Muskellunge larvae in length and weight on diets of *Artemia* and fish larvae. Both species could consume fish larvae as a first food. No transition from zooplankton was necessary. Wild Northern Pike and Muskellunge larvae consumed primarily zooplankton; Muskellunge consumed more fish larvae than did Northern Pike.

Recolonization of the upper Mississippi River basin by Muskellunge and Northern Pike after the retreat of the Wisconsin glacier (9,000–10,000 YBP) resulted in Muskellunge occupying some water bodies that Northern Pike did not. This disjunct distribution pattern was more prevalent in tributaries to lakes Michigan and Superior than in the lower Great Lakes (Inskip 1986). Stocking of Northern Pike in the 1930s in northern Wisconsin lakes, which previously had only Muskellunge, led to apparent declines in the Muskellunge population and Northern Pike stocking was discontinued there in 1941 (Oehmcke 1951). Stocking of Northern Pike continued elsewhere and had similar results. The decline of Muskellunge populations led to the perception that there was an inverse abundance relationship between Muskellunge and Northern Pike.

Several factors have been proposed to account for this relationship. Each of these factors represents a presumed advantage that Northern Pike have over Muskellunge: adhesive eggs and larvae that have adhesive papillae, faster growth from egg to juvenile, and the ability of the eggs and larvae to develop in colder water. If these factors do confer an advantage to Northern Pike, it may be more apparent in smaller water bodies. In large water bodies such as the upper St. Lawrence River, Northern Pike and Muskellunge can coexist. Both species are considered to be native (Crossman 1978) and fossil evidence suggests that they have coexisted here for at least the past 600 years (McAllister 1959). Their coexistence would suggest that any advantage that Northern Pike have over Muskellunge is less effective in the St. Lawrence River perhaps because the spawning and nursery habitat is more extensive and diverse than it is in small water bodies.

Northern Pike generally spawn just after ice-out at water temperatures between 4°C–11°C while Muskellunge spawn later when water temperatures are 9°C–15°C (Scott and Crossman 1973). The overlap of spawning temperature range may also result in an overlap of spawning activity (Williamson 1942; Farrell et al. 1996). Earlier spawning by Northern Pike could give them a headstart on growth and increase the potential for Northern Pike preying on the smaller Muskellunge larvae. Northern Pike are generally

larger than Muskellunge during the first year of life (LaPan 1985; Farrell 1998) which may reflect earlier spawning or a faster growth rate.

It has been presumed that Northern Pike eggs and larvae may survive better in areas of low dissolved oxygen and high turbidity or siltation due to the adhesive nature of their eggs and to the presence of adhesive papillae (cement glands) on the heads of the larvae. These characteristics would allow the eggs and larvae to become attached to vegetation above the substrate thereby avoiding areas of low-oxygen and heavy siltation.

Balon (1975) characterized the family Esocidae as phytophils (guild A.1.5) that are nonguarding, open substrate spawners. Representatives of this guild generally have adhesive eggs and the larvae possess adhesive papillae. Dombeck et al. (1984; 1986), however, attributed Muskellunge with having nonadhesive eggs and larvae that lacked the adhesive papillae seen in other esocids. Are Muskellunge unique in this regard in a family of fish that are similar in most characteristics? Other reports attribute Muskellunge eggs as being adhesive (Cooper 1983) and state that larvae have adhesive papillae (Leslie and Gorrie 1985).

The geographical distribution of Northern Pike extends farther north than that of Muskellunge (Crossman 1978), and this implies that Northern Pike eggs and larvae are more tolerant of colder water temperatures than Muskellunge are. If true, this could be reflected in faster development and growth by Northern Pike. The differences in spawning time could be related to temperature tolerance and would serve as a partial temporal segregator that could reduce competition during spawning.

The experiments described here attempted to utilize a 'natural' temperature progression as would be experienced by wild fish. Flynn Bay, a known Muskellunge and Northern Pike spawning area (LaPan and Werner 1989), was used as a model for what would be a natural temperature progression, and the temperatures in the experiments were compared to that (Flynn Bay was one of several bays being evaluated for Muskellunge restoration in another study; therefore adult fish from Flynn Bay were not

used in this study.) These experiments thus have a limitation in that water temperature was not controlled, although groups of fish that are compared have the same thermal history. Another approach would be to place artificially-spawned eggs (of known age) in Flynn Bay but this would require provision for preventing predation of the eggs with some kind of enclosure that would allow for sampling; the enclosure would also restrict water movement, which might promote the growth of algae (reducing oxygen in the enclosure) as well as restricting prey food items, leading to starvation of the experimental larvae. Wave action from wind could also overturn an enclosure and scatter the eggs. Sampling wild fish would result in a mix of unknown ages and thermal history.

There were two objectives in this study: 1) to determine the gross physical development of Northern Pike and Muskellunge from a series of eggs and larvae that had experienced the same thermal history and food items from egg fertilization through the juvenile stage; 2) to compare the effects of differing diets (brine shrimp *Artemia* compared to various species of fish larvae) on the total length–weight relationship of Northern Pike and Muskellunge larvae, and to determine which species of seasonally-available fish larvae could be consumed by Northern Pike and Muskellunge larvae. The first objective was accomplished with fish raised in 1994; the second objective was accomplished using fish raised in 1996, 1997 (pike only), and 1998. An additional series of Northern Pike and Muskellunge were raised on brine shrimp in 1998 as supplemental material for comparisons of development and length–weight relationships.

Methods

All of the objectives required obtaining eggs, which was done by capturing adult Northern Pike and Muskellunge in trapnets in the Thousand Islands region of the upper St. Lawrence River (Fig. 1) in May of 1994, and 1996–1998. Northern Pike, caught in Garlock and Deer Island bays (mean total length 580 mm; weight 2.5 kg), were spawned artificially in the field using the dry method (Sorenson et al. 1966; Klingbiel 1986). The milt from two or more male Northern Pike was used to fertilize the eggs of a single female Northern Pike resulting in multiple families of eggs that were pooled. Fertilized Northern Pike eggs were placed into coolers, allowed to water harden, and returned to the laboratory. Muskellunge was most often collected in spawning pairs (one male: one female) but no spawning pairs were caught in 1997 so no Muskellunge were raised in that year. Paired Muskellunge were transported from Blind Bay to the laboratory at Governors Island for spawning (dry method; single family) due to their larger size (mean total length 1165 mm; weight 13 kg) to avoid injury to the fish and the potential loss of eggs. All adult fish collected were returned to their point of capture.

Incubation of fertilized eggs was done in the same way for each of the experiments: Eggs were incubated

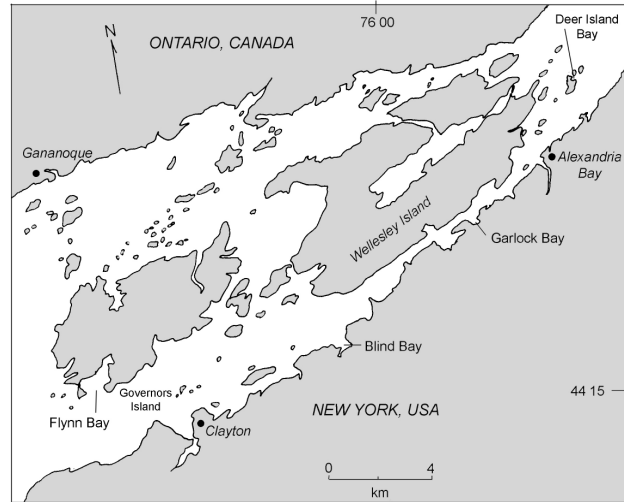


FIGURE 1.—Location of four bays, and the laboratory at Governors Island, in the upper St. Lawrence River. Flynn Bay is located at river kilometer 1088 and Deer Island Bay is at river kilometer 1064. River flow is to the northeast.

in hatching jars (Fig 2, left) in a flow-through system using filtered St. Lawrence River water, and transferred to 0.5 m³ tanks prior to hatching (Fig. 2, right). Tanks were cleaned each day. Diseases were controlled with formalin baths (1:600 for 15 min for eggs; 1:5000 for 1 h for larvae) and NaCl for juvenile fish (1% saturated brine by volume for 1 h). St. Lawrence River water (source water for incubation) was 2°C–3°C colder than that in Flynn Bay so a minimum water temperature was maintained at about 11°C and was allowed to fluctuate naturally above the minimum in response to weather conditions. Incubation water temperature, and that in Flynn Bay, was recorded daily in 1994 and by automatic recorder at 1-h intervals from 1996–1998.

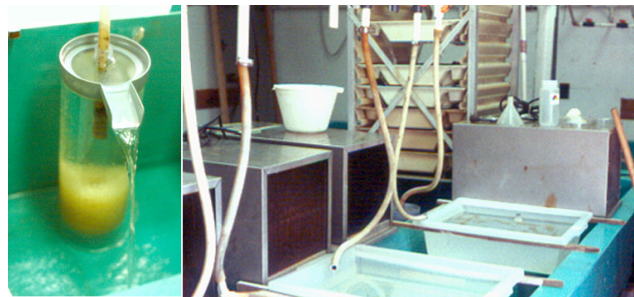


FIGURE 2.—Flow-through hatching jar (left) containing Northern Pike eggs and (right) plastic trays containing developing larvae, which also uses a flow-through system.

Observed development time (in hours) was converted to cumulative degree days (DD) by summing the difference between the mean daily water temperature and the lower temperature threshold for each species (threshold was 1°C for Northern Pike—determined by Kotylrevskaya (1969), and set arbitrarily at 2°C for Muskellunge). The threshold value represents the lowest water temperature at which development will occur: lower temperatures result in no

development regardless of incubation time (www.ipm.ucdavis.edu/WEATHER/ddconcepts). Although DD calculation started at fertilization, estimates of the DD required to reach specific developmental states were approximate since not all individuals reached the same developmental state over the same number of hours. DD and the corresponding fish lengths represented the first observed occurrence of the particular developmental state.

Objective 1.—Gross physical development of Northern Pike and Muskellunge eggs, larvae, and juveniles. The specific methods used for this objective were: Northern Pike and Muskellunge larvae were fed a diet of brine shrimp *Artemia* under variable fluorescent illumination. Eggs and larvae of both species were preserved in 10% buffered formalin for analysis of gross body morphology, pigmentation, and gut development. Presence of adhesive papillae was determined by microscopical examination. Those larvae used to estimate development of teeth, bones, and otoliths were preserved in alcohol, and a subset of larvae was cleared and stained (Fritzche and Johnson 1979) to examine teeth and bones, but not otoliths, which could be dissolved by the clearing process.

Morphological measurements were made on freshly-preserved fish under a dissecting microscope fitted with an ocular micrometer. Blood circulation patterns were determined by observing live specimens under a dissecting microscope at 15X. Attachment behavior was observed in each year by placing fish in a small aquarium divided by a glass partition. The partition provided an attachment surface that could be viewed from three directions and provided for an accurate determination of the attachment point. Illustrations of various phases of development were made freehand from preserved larvae under a dissecting microscope. Each illustration represents one individual thus the characteristics shown are not idealized or composites. Yolk volume (V) in fish larvae was determined using the equation for an ellipsoid mass:

$$V = 0.1667\pi LH^2$$

where L is length and H is height. Cannibalistic fish were removed from the experiments and not used in descriptions.

Objective 2.—Growth of Northern Pike and Muskellunge larvae on a diet of brine shrimp or fish larvae. The specific methods used for these objectives were: Recently-hatched Northern Pike and Muskellunge were subdivided into four groups of 80 fish each. Northern Pike and Muskellunge from two groups were fed brine shrimp and the other two groups were fed wild-caught fish larvae. The food type fed to each group was their first and only food type. The fish larvae used as prey were those that would be available seasonally to Northern Pike and Muskellunge in the wild. Prey fish were collected by dip-net from local bays and measured prior to being introduced to predators. Food was provided to Muskellunge from 18 June to 21 July, 1996, and to Northern Pike from 6 June to 28

June, 1997. A sample of five Muskellunge and five Northern Pike was taken once per week from each diet category. Total length (0.1 mm) and blotted wet weight (0.001 g) of each fish was recorded prior to preservation in 10% buffered formalin. Sampled fish were not replaced. The growth in total length and weight of experimental fish was compared to the growth of wild Northern Pike and Muskellunge larvae collected from various bays in 1992 and from 1996–1998.

Statistical tests were made using SAS version 8 (1988) at an overall alpha of 0.05. Comparisons of egg diameter, hatching length, and yolk volume used ANOVA with a Bonferroni correction for multiple comparisons. Regression (linear, quadratic, and power equations) and ANCOVA were used for comparing the relationship of total length and wet weight to age, with year as the covariate. Cook's influence statistic and the Durbin-Watson test for autocorrelation were also used.

Results

Objective 1.—Gross physical development of Northern Pike and Muskellunge eggs, larvae, and juveniles. The incubation water temperature varied by as much as 6°C during the first two weeks (Fig. 3) as a result of cold fronts and remained colder than the temperature in Flynn Bay, although the seasonal trend was similar.

Eggs of Northern Pike and Muskellunge were rounded but not always spherical: diameter of individual eggs varied as much as 10% in Northern Pike and 8% in Muskellunge. The greatest egg diameter was not consistent with the orientation of development occurring on the yolk in either species. The mean diameter of Northern Pike eggs from Deer Island Bay was significantly larger than the mean diameter of Northern Pike eggs from Garlock Bay, and the mean diameter of Muskellunge eggs was significantly larger than the mean diameter of Northern Pike eggs (Bonferroni *t*-test, critical *t*=2.45; *F*=69.9, *P*<0.0001), therefore the egg volume was similarly largest in Muskellunge, and Northern Pike egg volume from Deer Island Bay was larger than that from Garlock Bay (Bonferroni *t*-test, critical *t*=2.45; *F*=68.3, *P*<0.0001; Table 1).

Eggs of both species remained adhesive for 15–20 minutes after extrusion but were not adhesive after water hardening (about 30 min). The chorion of the Northern Pike egg had a slightly dimpled appearance at 25–50X and closely spaced nodules could be seen at 400X (Johnson and Werner 1986). These nodules were smaller in a circular area around the micropyle which was visible (at 25X) as a relatively smooth and flattened area on the chorion. Muskellunge eggs had a rougher chorion than Northern Pike eggs. Plugs could be seen easily at 25X and nodules could be seen at 50X. Perivitelline space varied from 0.3–0.5 mm in fertilized Northern Pike eggs from Garlock Bay

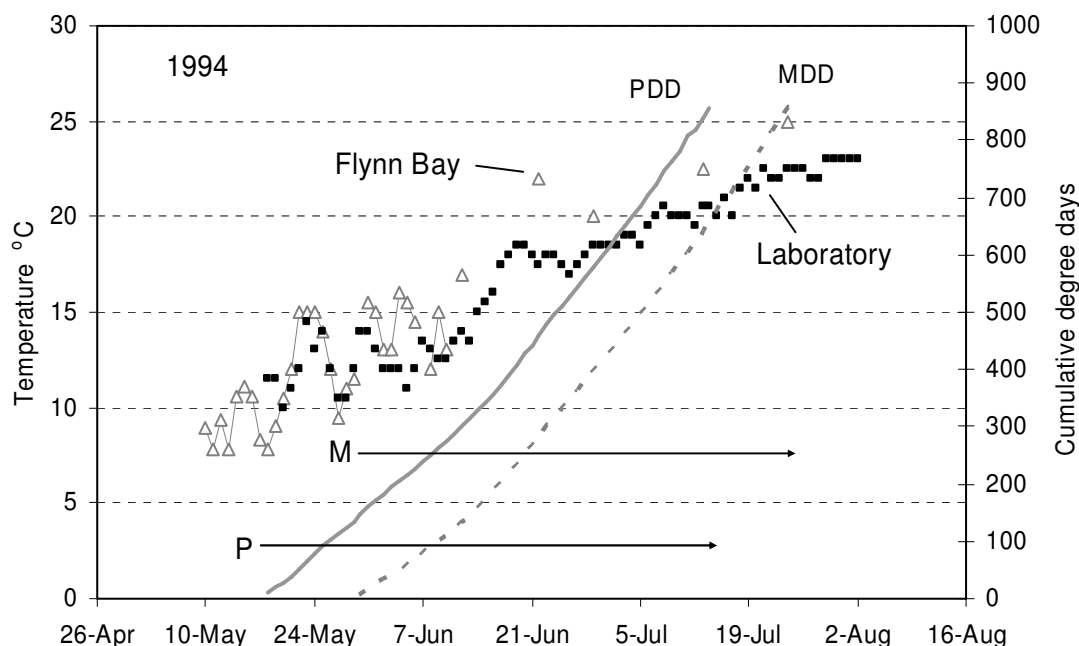


FIGURE 3.—Incubation water temperature for Northern Pike and Muskellunge (black line) in 1994, and natural water temperature (triangles) in Flynn Bay. PDD and MDD refer to cumulative degree days for Northern Pike (gray solid line) and Muskellunge (dashed line). Arrows indicate the incubation period for Northern Pike (P) and Muskellunge (M).

and was 0.1 mm in fertilized Northern Pike eggs from Deer Island Bay (Fig. 4). Perivitelline space ranged from 0.17–0.42 mm in Muskellunge eggs (Fig. 5). The yolk of both species was pale amber in life and pale yellow after preservation in formalin. Large, clear cells similar to those observed in walleye (McElman and Balon 1985) were observed in eggs of both species.

TABLE 1.—Mean diameter (\pm SE), range, and volume of Northern Pike and Muskellunge eggs. Mean diameter was significantly different ($F=69.9$, $P<0.0001$) in each column as was mean egg volume ($F=68.3$, $P<0.0001$). $N=27$ eggs in each column.

	Northern pike		Muskellunge
	Garlock Bay	Deer Island Bay	Blind Bay
Mean egg diameter	2.80 ± 0.02	2.99 ± 0.01	3.07 ± 0.01
Range	2.58–3.17	2.92–3.08	2.92–3.17
Mean egg volume	$11.5 \text{ mm}^3 \pm 0.29$	$14.03 \text{ mm}^3 \pm 0.17$	$15.18 \text{ mm}^3 \pm 0.21$

The first body movements were observed at 75 DD in Northern Pike embryos and at 88 DD in Muskellunge. These movements were restricted to flexing of the tail, which increased as the embryos neared hatching. The

pectoral fin buds, adhesive papillae, rudimentary gut, dorsal and anal finfolds, and gill slits were present prior to hatching. The developmental changes from fertilization to hatching are summarized in Table 2.

Heart.—The heart was visible, but not beating, at 62 DD in Northern Pike embryos and at 88 DD in Muskellunge embryos (Table 2). The heart was located under and to the left of the longitudinal axis of the body just posterior to the optic cup (Fig. 4e and 4f; Fig. 5e and 5f). The heart was beating at 71 DD in Northern Pike, and at 109 DD in Muskellunge. The heart beat rate was similar in both species at 60 beats per minute at 13°C and increased to 120 beats per minute in embryos at 15°C. Limited blood circulation was visible on the yolk around the heart region and along the ventral margin of the tail in embryos that were close to hatching.

Adhesive papillae.—These structures were first seen in Northern Pike embryos at 75 DD from Garlock Bay and at 70 DD in Northern Pike embryos from Deer Island Bay. Papillae were first visible in Muskellunge embryos at 109 DD. The area covered by papillae increased in size in both species as the embryos developed. The largest papilla extended outward 0.04 mm away from the body in Northern Pike but only 0.02 mm in Muskellunge. Papillae were located in a semi-circular patch ventral to the eyes (Fig. 6). Papillae were present in Northern Pike up to 12 mm and in Muskellunge up to 14 mm. The papillae were reduced in size, and in area, after the gas bladder was filled.

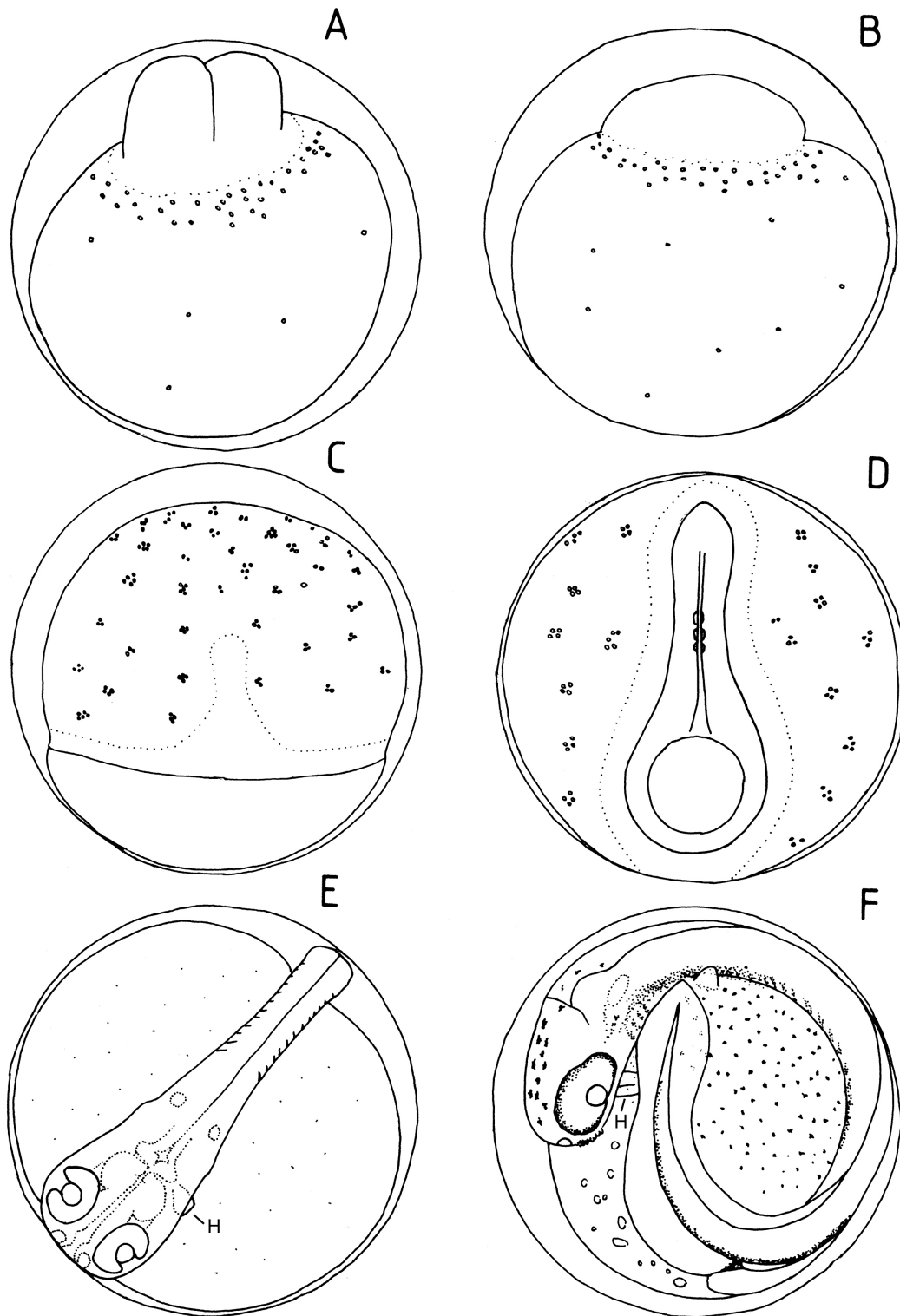


FIGURE 4.—Development of Northern Pike eggs from Garlock Bay incubated in 1994: A) two-cell stage at 6 hours; B) blastula at 26.5 hours; C) gastrula and formation of embryonic shield at 74 hours; D) neural keel with three pairs of somites at 96 hours; E) embryo with optic cups at 127 hours, heart (H) is located between the optic cup and auditory vesicle; F) embryo just before hatching at 182 hours, the heart is located to the right of the eye.

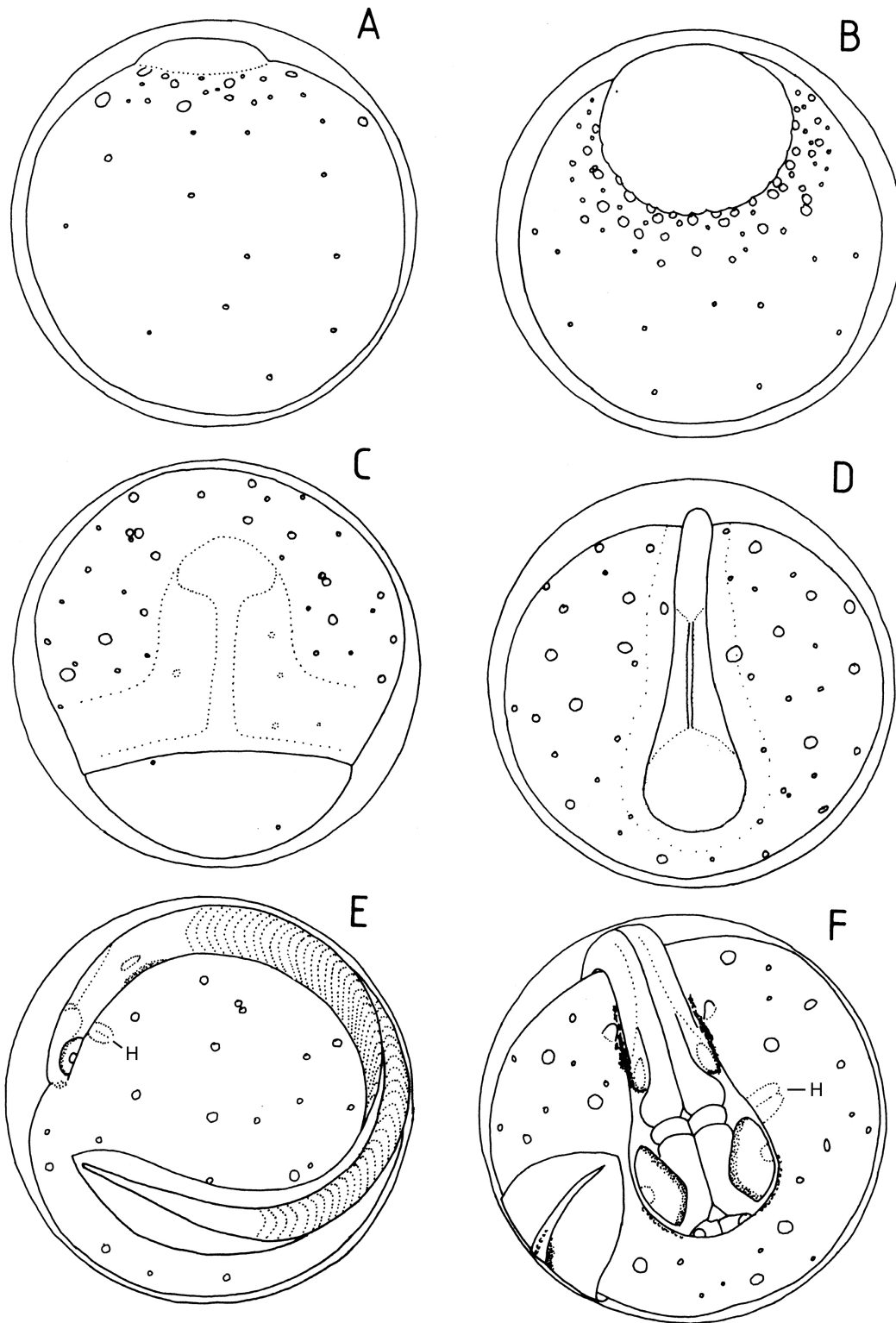


FIGURE 5.—Development of Muskellunge eggs from Blind Bay incubated in 1994: A) single-cell stage at 7 hours; B) 64-cell stage at 22 hours, oil droplets surround the blastomeres; C) gastrula and embryonic shield at 87 hours; D) neural keel at 101 hours; E) embryo with developing heart (H) posterior to eye at 196 hours; F) embryo before hatching at 278 hours, heart is located to the right of the eye.

Northern Pike and Muskellunge development, growth, and food

TABLE 2.—Elapsed time (hours and degree-days: DD) from fertilization to the first formation of structures or occurrence of events in Northern Pike and Muskellunge raised in 1994.

Structure or event	Northern pike				Muskellunge	
	Garlock Bay		Deer Island Bay		Blind Bay	
	Hours	DD	Hours	DD	Hours	DD
4-cell	7	13	6	12	15	14
16-cell	26	22	21	20	18	15
Half completion of gastrulation	74	42	50	31	80	42
Neural keel	87	44	59	34	111	58
Somites	98	55	68	39	136	59
Heart formation (not beating)	120	62	120	66	219	88
Optic cups with lenses, auditory vesicles and						
Olfactory cups	127	71	126	70	196	78
Beating heart	127	71	126	70	255	109
Tail-free embryo	133	75	126	70	196	78
Adhesive papillae	133	75	126	70	255	109
Pectoral fin buds	156	88	149	84	269	113
Blood circulation	178	99	157	88	255	109
Gill slits	178	99	157	88	219	88
Hatching	184	102	164	92	303	132

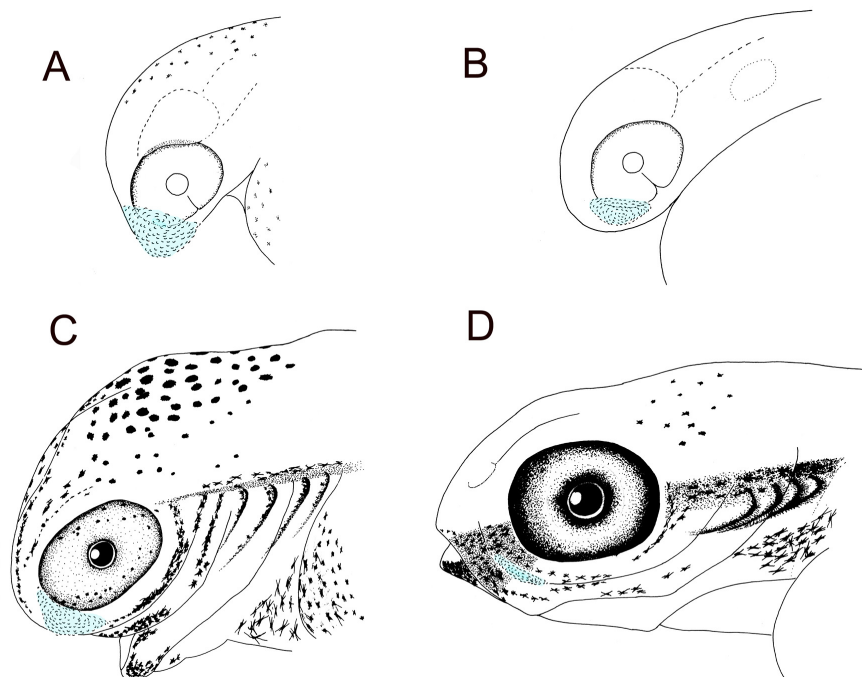


FIGURE 6.—Location of adhesive papillae (blue shading) in 7.5 mm Northern Pike (A), 8.5 mm Muskellunge (B), 10.5 mm Northern Pike (C), and 13 mm Muskellunge (D).

Muskellunge larvae exhibited attachment behavior for 4 days while Northern Pike exhibited the attachment behavior for 7 days.

Pigmentation of embryos.—Melanophores were first seen along the dorsal margin of the eyes at about 70–75 DD in Northern Pike embryos and at 109 DD in Muskellunge embryos. Pigmentation was more extensive on the dorsal surface of the yolk sac in Northern Pike embryos but was found only near the pectoral fin buds in Muskellunge embryos. Yolk sac pigmentation was restricted to the ventral area near the anal finfold in Muskellunge.

Oil globules.—Northern Pike and Muskellunge yolks contained numerous oil globules of a similar diameter (approx. 0.04 mm); some oil globules in Muskellunge eggs began to coalesce into groups or larger globules of 2–3 times greater diameter at 44 DD.

Hatching began in Northern Pike at 102 DD (Garlock Bay) and 92 DD (Deer Island Bay) after fertilization, and in Muskellunge at 132 DD. Hatching continued for 6–8 h in Northern Pike and for 60 h in Muskellunge. Most larvae hatched head first, but there were some that hatched tail first. The heads in Muskellunge embryos were flattened prior to hatching and, after hatching, increased in height from 0.21 mm to 0.58 mm and decreased in width from 1.08 mm–0.96 mm. These changes were not observed in Northern Pike embryos.

Development of Northern Pike and Muskellunge larvae.—Northern Pike from Garlock Bay hatched at a mean total length of 7.5 mm \pm 0.17 mm (range 7.25–7.67 mm, n=15) and from Deer Island Bay at a mean of 8.15 mm \pm 0.18 mm (range 8–8.33 mm, n=15). Muskellunge hatched at a mean length of 8.45 mm \pm 0.24 mm (range 8.16–8.83 mm, n=15). Mean hatching length was significantly larger in Northern Pike from Deer Island Bay than Northern Pike from Garlock Bay and Muskellunge hatching length was significantly larger than Northern Pike hatching length ($F=112.6$, $P<0.0001$). The head was deflected forward over the yolk sac at hatching in both species but moved upward and away from the yolk sac over the next 2 h (Fig. 7). Both species showed similar behavior after hatching: lying quiescently on their yolk sac on the bottom with brief and intermittent movement of the tail, becoming more active as the yolk was utilized.

Yolk absorption.—The yolk in both species was large and oblong at hatching. Yolk length and depth was approximately 41% and 26% of TL in Northern Pike, and 45% and 25% of TL in Muskellunge. Utilization of the yolk resulted in a gradual decline in mean yolk depth but less change in mean yolk length in both species until the yolk was nearly depleted. The yolk was located on the left side (in dorsal view) of the gut cavity with the developing gut occupying the right side. Mean yolk volume was significantly larger ($F=13.86$, $P<0.0001$) in Muskellunge (5.01 mm³) than that in Northern Pike from Garlock Bay (3.91 mm³) and Deer Island Bay (3.23 mm³); mean yolk

volume in Northern Pike from Garlock Bay was significantly larger than that in Northern Pike from Deer Island Bay ($P<0.0005$). Yolk volume declined more rapidly in Muskellunge than in Northern Pike (Fig. 8). The yolk was absorbed at 275 DD (16 days post-hatching) in Northern Pike from Garlock Bay, at 226 DD (14 days post-hatching) in Northern Pike from Deer Island Bay, and 317 DD in Muskellunge (12 days post-hatching).

Heart and blood circulation.—The heart remained on the yolk sac and to the left of the head until about four days after the embryos hatched. As the head continued to develop, it moved farther away from the yolk which created a space between the head and the yolk. During this period, the heart assumed a position completely under the body anterior to the gill slits. Heart beat rate was approximately 120 beats per min.

Blood circulation was similar in recently-hatched Northern Pike and Muskellunge. Blood flowed from the heart through the area of the gill slits toward the tail along the ventral side of the notochord. Blood returned toward the heart through the caudal vein which branched near the anus to empty into the intestinal vein. No circulation was visible in the head region or dorsal to the notochord. Blood streamed forward in the intestinal vein from the caudal finfold across the intestine and along the ventral portion of the intestine. The intestinal vein branched to form an extensive network of capillaries across the yolk sac (Fig. 9). Flow decreased at the heart and formed a pool of blood to the left of the heart.

Blood flow was more extensive in Northern Pike at 14 mm (Fig. 10). Blood could be seen flowing from the heart to and around the gill filaments (but not lamellae) and forward toward the eyes. Blood flowed dorsally to the developing vertebrae and between each vertebra in alternating directions. The dorsal flow could not be seen for the full length of the body. Bidirectional flow was visible along the ventral margin of the caudal area and formed a braided stream in a pigmented area where mesenchyme rays first appeared. The ventral flow continued forward around the posterior and anterior sides of the anus and then along the dorsal margin of the gut toward the heart. Blood circulation was obscured in Muskellunge larvae longer than 11.5 mm, especially along the ventral margin of the body and along the notochord. Blood circulation was visible along the ventral margin of the posterior body, along the ventral part of the intestine and the yolk sac (Fig. 10). The capillary network on the yolk sac was reduced in size with fewer but larger capillaries. The ventral-most capillary carried most of the blood flow from the intestinal vein to the heart.

Pigmentation from 8.0–13.5 mm.—Northern Pike larvae were more heavily pigmented at hatching than were Muskellunge larvae. Body pigmentation on Northern Pike embryos consisted of small but dense melanophores along the dorsal margin of the gut and eyes, and larger, but fewer,

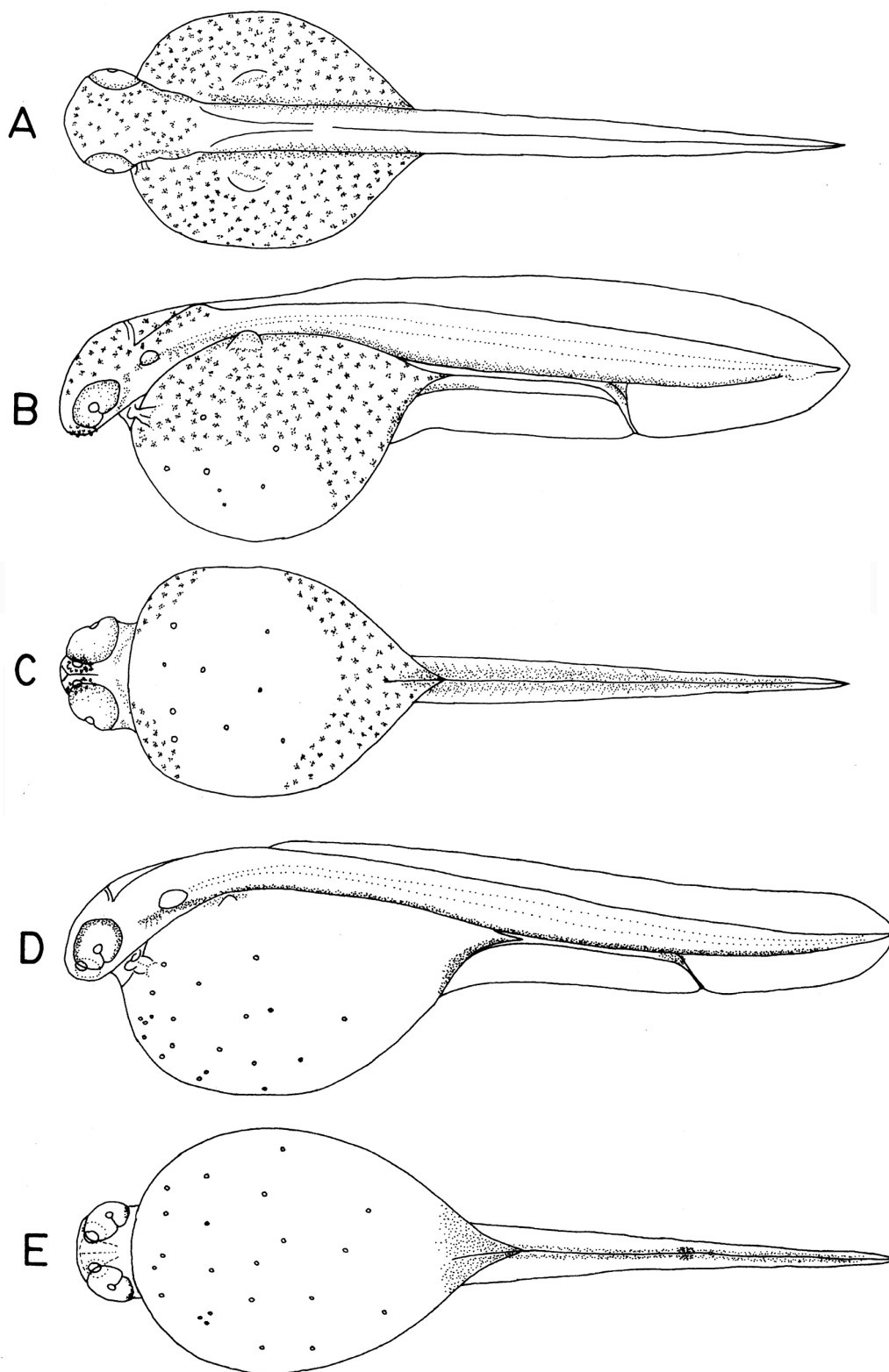


FIGURE 7.—Dorsal, lateral, and ventral views of 8 mm Northern Pike larva 2 hours after hatching (A to C). The heart is located on the yolk sac posterior to the eye. Papillae are visible under the eyes. Lateral and ventral views of 8.2 mm Muskellunge larva (D and E) 2 hours after hatching. Papillae are represented by stippling.

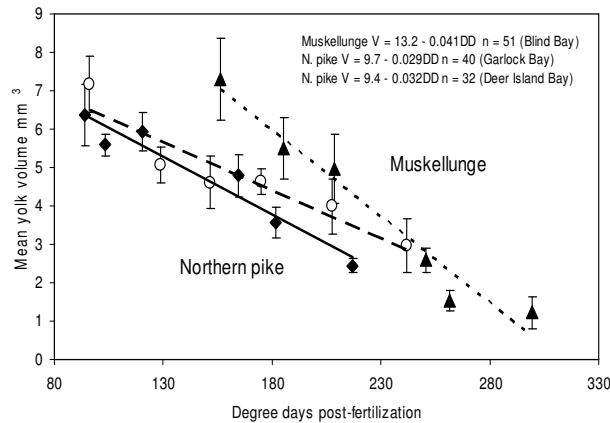


FIGURE 8.—Changes in mean yolk volume (V in equations) in relation to degree days for Muskellunge (triangles, $r^2 = 0.95$), Northern Pike from Garlock Bay (open circles, $r^2 = 0.91$), and Northern Pike from Deer Island Bay (diamonds, $r^2 = 0.93$). Bars represent one SE.

melanophores on the head and dorsal surface of the body. Melanophores covered approximately 80% of the Northern Pike yolk sac at hatching but were absent from the most ventral portion of the yolk sac: the melanophores were drawn together (Fig. 11) as the yolk was utilized. Body pigmentation on Muskellunge embryos was found along the ventral body margin, on the posterior intestine, with scattered melanophores on the surface of the yolk sac. Both species had internal melanophores along the notochord just below the auditory vesicles. Internal pigmentation on the developing gill arches was present only in Northern Pike embryos prior to hatching. Eyes of both species were pigmented at the outer margins at hatching, and eye pigmentation was complete at 170 DD in Northern Pike (10 mm) and at 252 DD in Muskellunge (13 mm). Muskellunge larvae became darker as they grew due primarily to an internal band of pigment that extended from anterior of the auditory vesicles, around the gill slits (and later, the arches) to the pectoral fin buds. An external band was present along the ventral margin of the body to the tail. The external band of melanophores was darker at the leading edge of the myomeres in both species. The lateral band of pigmentation increased in density and in size as Muskellunge increased in length but became more diffuse in Northern Pike larvae longer than 12 mm. A small area of pigmentation on the dorsal surface of the tail was present in Muskellunge at 9.4 mm and had increased at 11.5 mm (Fig. 12) but was not present in Northern Pike. Both species had melanophores in the caudal area where the hypural and epural elements would form but melanophores were denser in Muskellunge larvae.

Pigmentation from 14–24 mm.—Many large melanophores covered the dorsal surface of the head in Northern Pike larvae and extended posteriorly to directly above the cleithrum where the size of the melanophores decreased; these smaller melanophores formed parallel rows

on either side of the dorsal surface of the body (Fig. 13), and were more distinct in larger Northern Pike. Small melanophores covered the stomach and anterior lateral body surface and posteriorly along the gut. An internal band of dense pigment was present on the dorsal surface of the gut. Pigment patterns in Muskellunge shared many of the characteristics seen in Northern Pike: Eye bars which extended onto the snout, patches of large melanophores over the brain, and parallel rows of melanophores along the dorsal surface of the body (Fig. 14). The lateral body pigment band in Muskellunge larvae became darker and wider as larvae increased in length up to 24 mm. The lateral pigment included internal and external pigment in the eye bar, internal pigment along the notochord and gill arches, and internal and external pigment from the cleithrum to the tail.

The stomach surface of Northern Pike larvae (Fig. 15) had less internal pigment than did Muskellunge larvae. Melanophores were present on the isthmus, between the pectoral fins, and in a narrow longitudinal band on the stomach (Fig. 15) of Northern Pike larvae at 22 mm. Similar pigment patterns were observed in Muskellunge larvae with the exception of the longitudinal band on the stomach.

Pigmentation at 30, 54, and 110–130 mm.—Body pigmentation in 30 mm Northern Pike was denser and more extensive than in shorter Northern Pike larvae particularly on the dorsal and lateral body above the lateral line (Fig. 16). The body pigmentation in 54 mm Northern Pike (Fig. 17) showed the initial stages of the more familiar vertical bars seen in longer fish. Muskellunge at 30 mm and 54 mm retained the lateral body pigment band seen in shorter larvae. Lateral body pigmentation at fish lengths >100 mm consisted of bars and large spots which are common in the Great Lakes strain of Muskellunge (Fig 18).

Finfolds, fins, and finrays.—The depth of the dorsal and anal finfolds nearly equalled the body depth in recently-hatched Northern Pike and Muskellunge, and were covered by large, clear cells (McElman and Balon 1985). Finfold absorption was completed in Northern Pike and Muskellunge at lengths greater than 30 mm. Pectoral fin buds were the first to emerge (Table 2) but were last to develop rays at fish lengths of 25 to 30 mm in both species. The shape of the pectoral fin did not assume the adult form until fish were longer than 54 mm. The caudal fin had a three-lobed outline with the smaller lobe surrounding the tip of the urostyle. The urostyle, and its fin lobe, remained prominent in 30 mm fish of both species. The caudal and pelvic fins assumed a more adult-like form at fish body lengths of 54 mm. Fin development is summarized in Table 3.

Gills, gill arches, and branchiostegal rays.—Gill slits were present at hatching in both species but the arches were not visible until 2 days after hatching. Short gill filaments were visible in Northern Pike at 172 DD (Table 3) and in Muskellunge at 187 DD. Denticles formed on the first gill arch in Northern Pike at 216 DD and in Muskellunge at 360

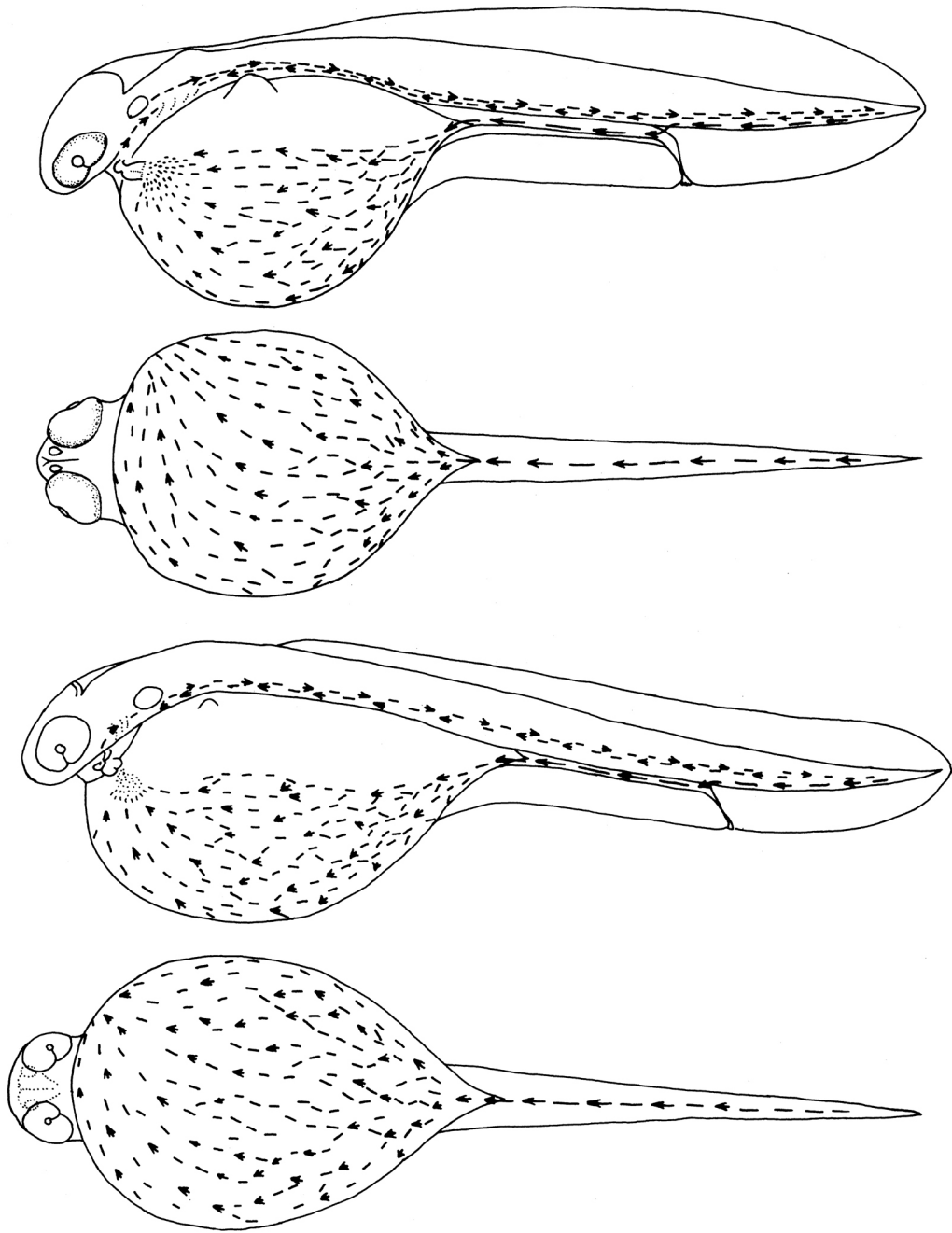


FIGURE 9.—Blood circulation in Northern Pike (Deer Island Bay) at 8 mm (upper pair) and in Muskellunge (Blind Bay) at 8.2 mm (lower pair). Arrows denote direction of blood flow and length of arrows indicates relative flow velocity.

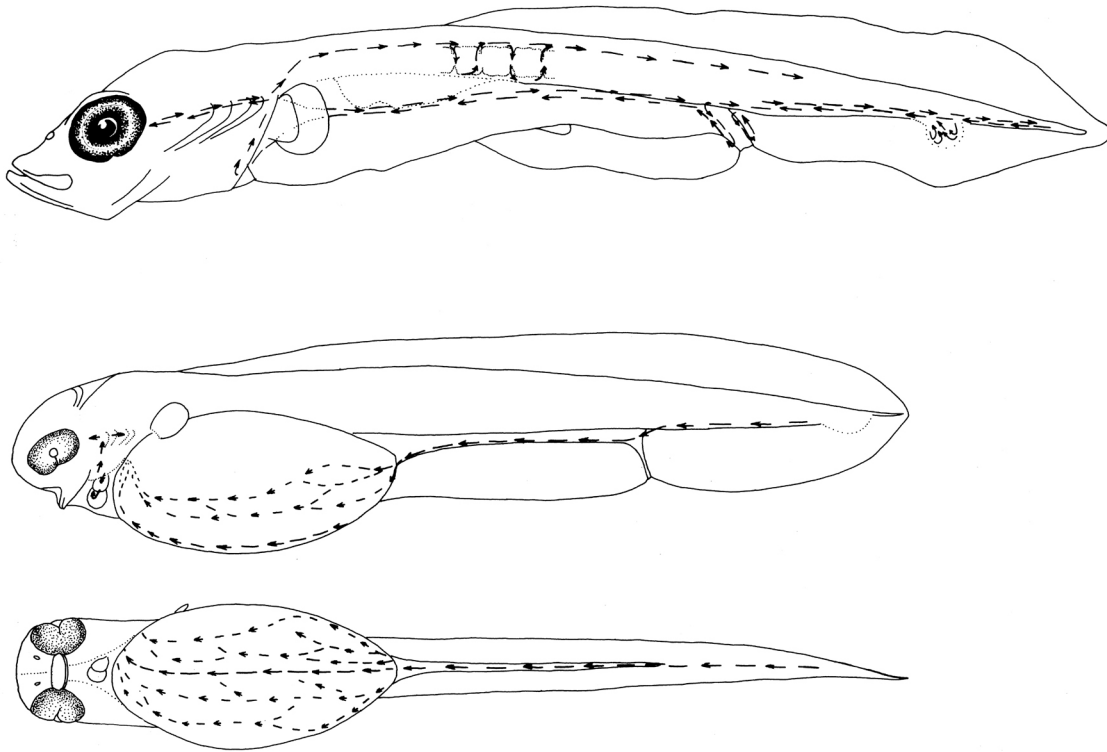


FIGURE 10.—circulation in Northern Pike (Deer Island Bay) at 14 mm (upper figure) and in Muskellunge (Blind Bay) at 11.5 mm (lower figures). Arrows denote direction of blood flow and length of arrows indicates relative flow velocity. Only part of the circulation around vertebrae is shown.

DD. Denticles were often paired and formed first at the posterior end of the lower arches. Denticles were between 0.06 and 0.08 mm in height in 33 mm fish, and 0.1 mm in height in 48 mm fish. Branchiostegal rays formed first on the epihyal bone in both species and the minimum adult complement was reached after 562 DD in Northern Pike and after 770 DD in Muskellunge.

Mouth, teeth, and cartilage.—The mouth began as a fine line in both species extending between the eyes just anterior to the conjunction of the yolk sac membrane and the tissue of the head. The developing mouth was visible only in the ventral view. The mouth opened in 9 mm Northern Pike at 124 DD and in 10 mm Muskellunge at 187 DD. The mouth opened first at the center and advanced toward the eyes. The opening of the mouth coincided with the formation of two large teeth on the anterior edge of the vomer in both species. Smaller teeth (<0.1 mm) formed on the palatines, dentary, and the upper and lower pharyngobranchials when fish were between 11 and 12 mm TL (11 mm Northern Pike at 205 DD; 11 mm Muskellunge at 234 DD; 12 mm Northern Pike at 251 DD; 12 mm Muskellunge at 259 DD). Two rows of paired teeth, approximately 0.06 mm in height, were present on the palatines, 5–6 pairs of teeth on each side of the dentary (0.06 mm in height), and six large teeth (0.08 to 0.1 mm in height) on the vomer at 317 DD. Three to four pairs of teeth (0.08 mm in height) were present on

the upper and lower pharyngobranchials of 17 mm Northern Pike (370 DD) and Muskellunge (379 DD) and these teeth were more massive than the other teeth. All of the teeth were straight with sharp points. Replacement teeth could be seen at most tooth positions on the dentary and palatines. The shape and height of the teeth had differentiated in Northern Pike and Muskellunge at 21–24 mm (Northern Pike at 446–460 DD; Muskellunge at 533–640 DD): the vomerine teeth (0.12 to 0.14 mm in height) now faced posteriorly and those on the palatines faced inward. Teeth on the dentary were more rounded (0.1–0.12 mm in height) and faced slightly inward, and the pointed teeth on the pharyngobranchials (0.12 mm in height) were curved posteriorly. The teeth on the pharyngobranchials were evident in two patches, one forward of the other with the larger teeth (in height) at the posterior position. Tongue teeth were first seen in both species (Table 3) as two patches: one tooth in the center of the tongue and the remainder at the back of the tongue. Both patches were contiguous and contained 25 to 35 teeth at fish lengths between 30 mm–40 mm (577–600 DD).

Cartilage formed first in the head coinciding with the formation of teeth and the development of the branchial chamber. Cartilage had formed in the eye ring, forward end of the parasphenoid, dentary, palatines, palatoquadrate, hyomandibular, ceratohyal, and the basibranchial and

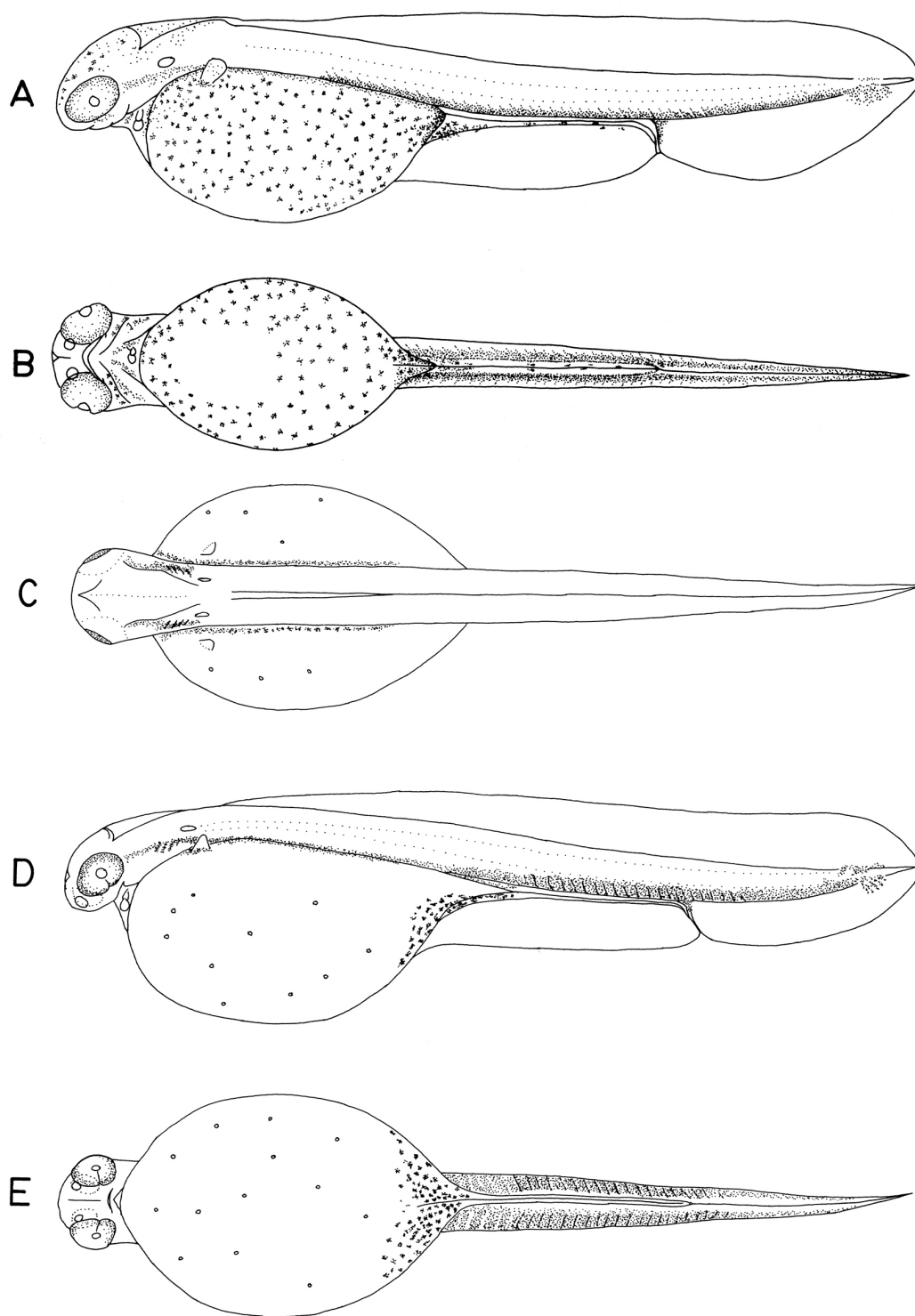


FIGURE 11.—Dorsal, lateral, and ventral views of a 10.4 mm Northern Pike larva (A to C, Deer Island Bay). The mouth is open and is located between the eyes in the ventral view (B). Lateral and ventral views of a 9.4 mm Muskellunge larva (D and E) from Blind Bay, where the mouth is not open but is visible as a line between the eyes in the ventral view (E). Stippling represents adhesive papillae.

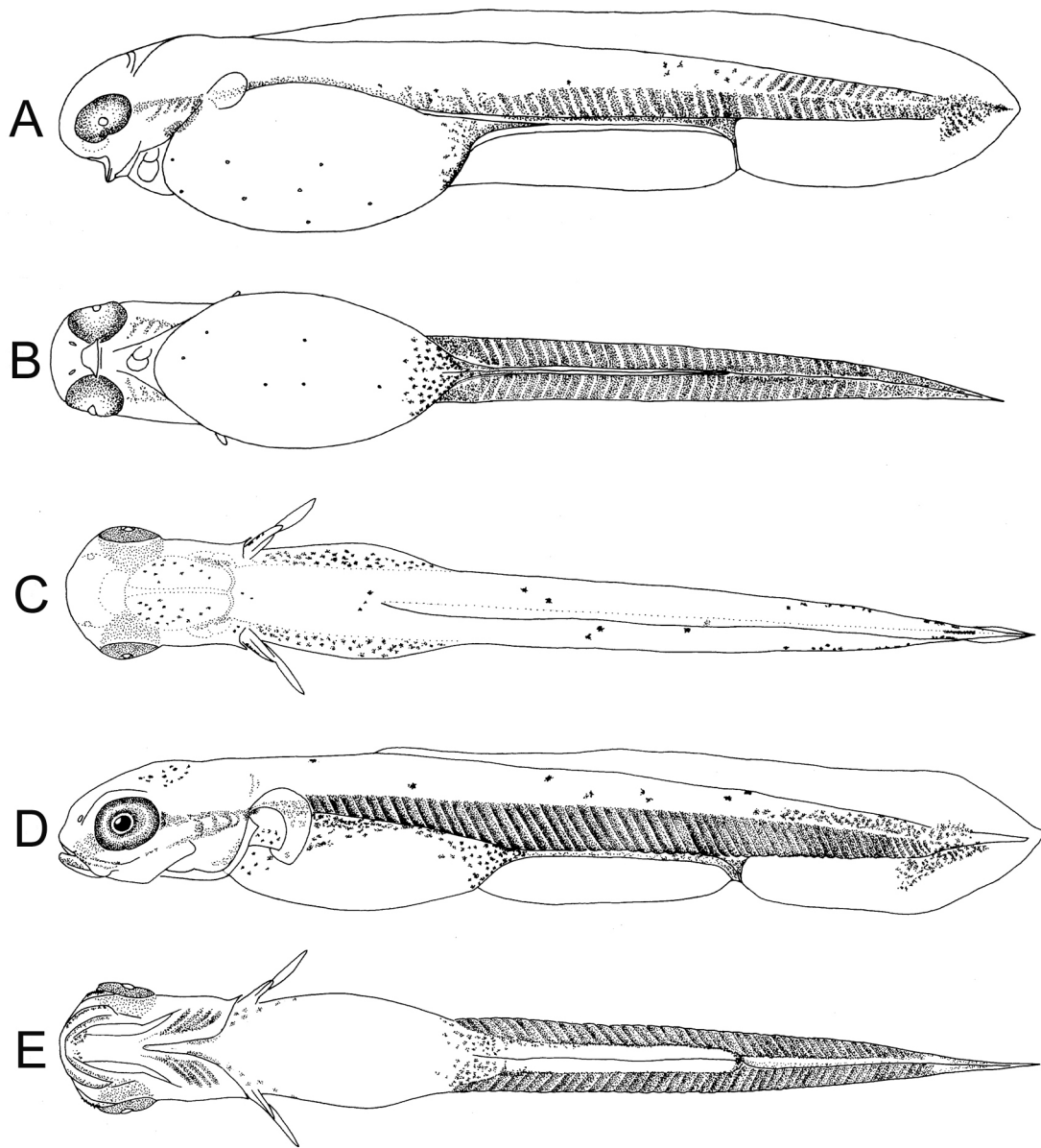


FIGURE 12.—Lateral and ventral views of a 11.5 mm Muskellunge larva (A and B). The stippled area under the eye in the lateral view represents the adhesive papillae; and dorsal, lateral, and ventral views of a 13.5 mm Muskellunge larva (C to E).

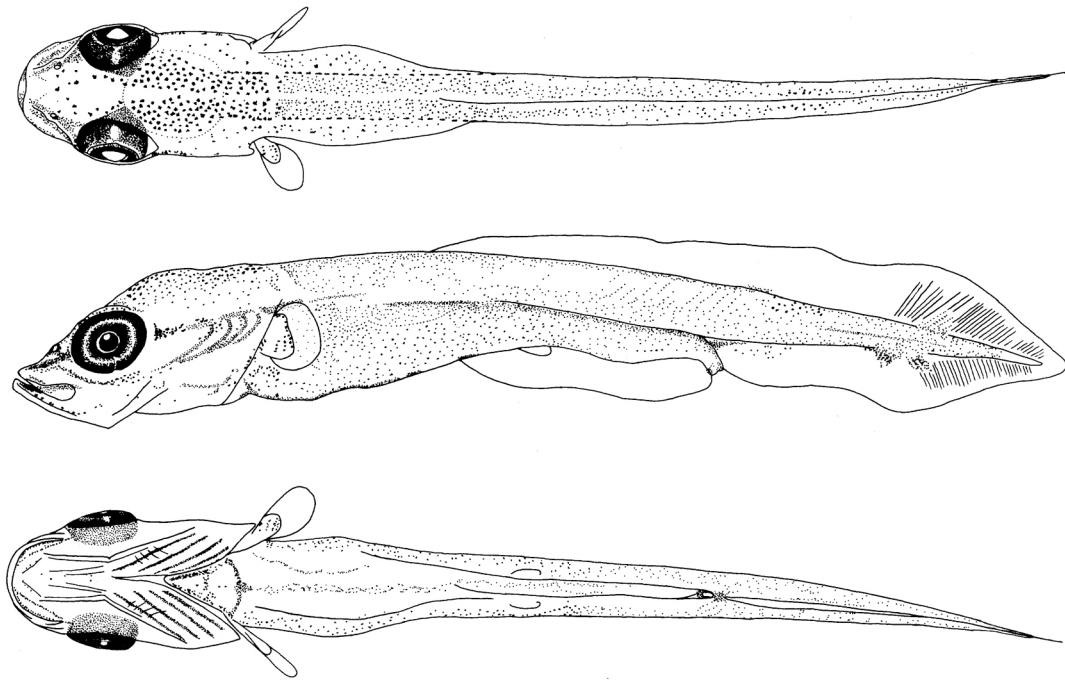


FIGURE 13.—Dorsal, lateral, and ventral views of a 14.5 mm Northern Pike larva from Garlock Bay. Mesenchyme rays are present in the caudal fin.

ceratobranchials in the branchial chamber in Northern Pike at 12 mm. Cartilage had formed in the same structures in 15 mm Muskellunge with the exception of the eye ring. The coracoid, scapula, and postcleithrum and two radials were developed in the pectoral fins at 12 mm in Northern Pike and at 15 mm in Muskellunge. The epibranchials, orbitonasal, and pharyngobranchials were evident at 15 mm in Northern Pike and at 19–22 mm in Muskellunge, and the hypural elements were developed in the caudal region as well as several neural spines. The full complement of neural spines was developed, as well as pterygiophores, in the dorsal and anal fins, and the pterygoid bone in Northern Pike at 21 mm, and in Muskellunge at 26–29 mm. The premaxilla, pelvic girdle, epural and hypural elements were complete in Northern Pike at 43 mm and in Muskellunge at 50 mm.

Otoliths.—The sagittae and lapilli were visible in the auditory capsules of recently-hatched larvae (8 mm) but were not examined. The sagittae in 14.5 mm Northern Pike had indistinct cores with non-continuous rings (Fig. 19a) with a rough surface crossed by ridges extending from the approximate center to the outer margin. The lapilli also had indistinct cores with rings that were visible only on the inward facing margin. The cores were rough with many small nodules transected by ridges. Growth of sagittae in 22.5 mm Northern Pike was greatest in the posterior direction, equal in anterior and dorsal directions, and least in the ventral direction (Fig. 19b). The rostrum and antirostrum were evident with the sulcus between them. The sagittae had nearly doubled in length, but not width, from

those in 14.5 mm Northern Pike. Growth rings were indistinct except at the edges and the center in sagittae from 47 mm Northern Pike (Fig. 19c). Much of the surface was uneven with many ridges and small, raised areas. The rostrum and antirostrum were prominent and the sulcus was deep. The rings in the lapilli were visible with transmitted light at 100X but not with reflected light at 50X. There was a wide area with no visible rings toward the anterior margin. The asterisci had developed in 47 mm Northern Pike and were generally rounded with a dorsally-projecting point. The asterisci were located directly behind the sagittae. The sagittae in 122 mm Northern Pike had no visible growth rings and the outline and surface was rough with many small projections (Fig. 19d). The lapilli were rough with rounded lateral projections in several planes around the margins, with a single smooth area near the center. No growth rings were visible. The asterisci were triangular in cross-section unlike the rounded asterisci in smaller Northern Pike. The surfaces were smooth with a distinct crystalline appearance that ran from the center toward the ventral margin. Sagittae in 14 mm Muskellunge were roughly rectangular with a distinct focus, continuous growth rings, and had a smooth surface broken only by numerous ridges extending outward (Fig. 20a). The lapilli were similar to the sagittae in shape and characteristics. The sagittae had doubled in length and width in 28 mm Muskellunge. The focus remained distinct but the growth rings were no longer continuous visually (Fig. 20b). The sulcus was evident but not deep. The surface of the sagittae and the lapilli were smooth except for the ridges. Growth rings were distinct only at the center and

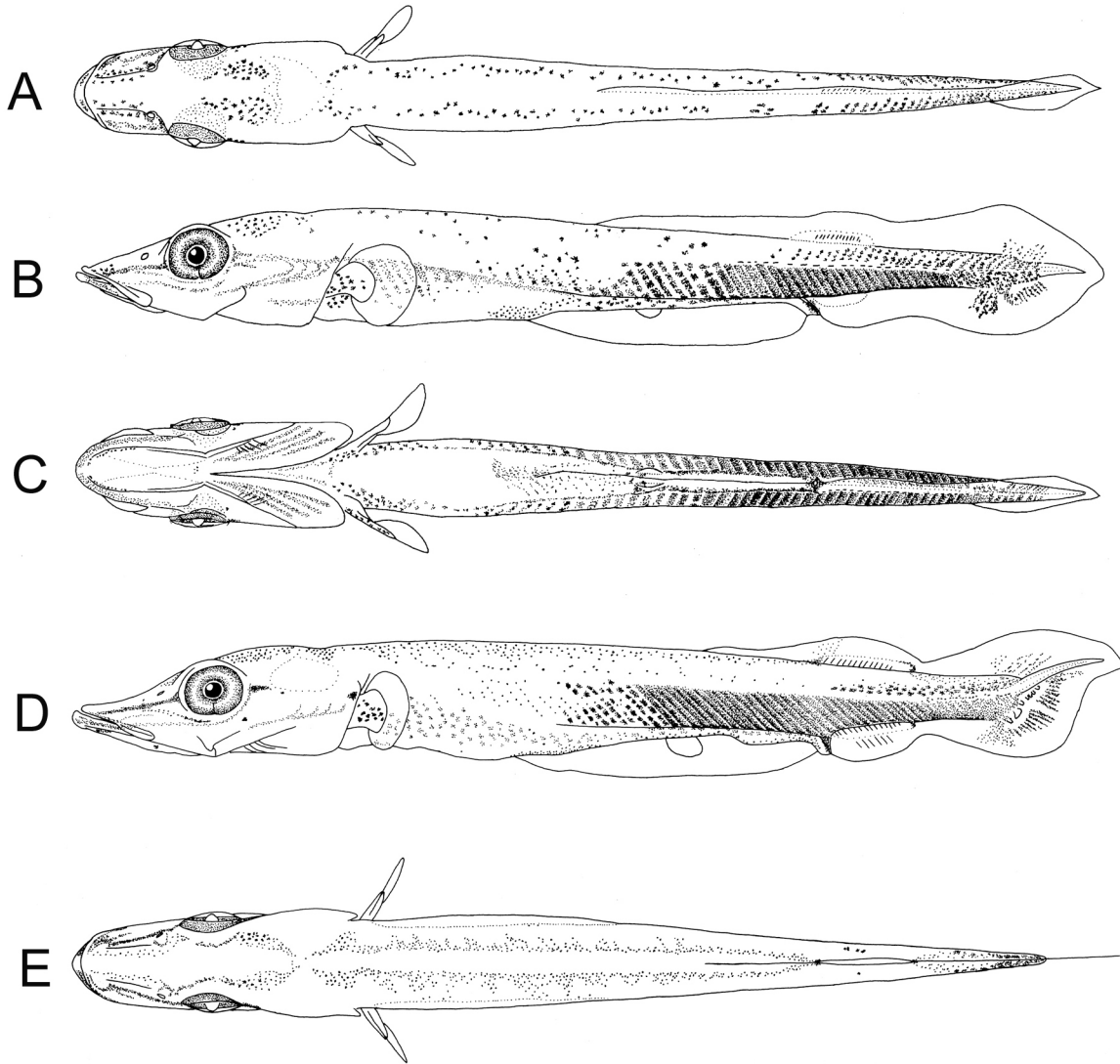


FIGURE 14.—Dorsal, ventral and lateral views of a 17.5 mm Muskellunge larva (A to C); and lateral and dorsal views of a 23.6 mm Muskellunge larva (D and E).

on one projection in sagittae in 50 mm Muskellunge (Fig. 20c). The rostrum, antirostrum, and sulcus were more defined and the surface had become rougher with many wide, flat ridges. Growth rings in the lapilli were no longer distinct and there were several small projections around the margins as well as on the surface. The lengths of the sagittae and lapilli in 50 mm Muskellunge were nearly proportional to that in 28 mm Muskellunge. Growth rings were visible at the focus and along one part of the outer margin in sagittae but only on the outer margin of lapilli in 122 mm Muskellunge (Fig. 20d). The asterisci were present and had the appearance of many longitudinal layers. There were no visible growth rings and the posterior surface consisted of

small rounded projections generally following the longitudinal layers. The interior surface was smooth.

Digestive tract and gas bladder.—The alimentary tract in recently-hatched Northern Pike (Fig. 21a) and Muskellunge (Fig. 22a) was essentially an undifferentiated tube with a slightly enlarged area where the stomach would form. The developing liver was located directly below the forming stomach. Differentiation of a sphincter in the hind gut, emergence of the gas bladder, and the enlargement of the liver was evident in the tract in 10.5 mm Northern Pike (Fig. 21b) and in 10.2 mm Muskellunge (Fig. 22b). Considerable folding of the gut mucosa had occurred in 11.8 mm Northern Pike (Fig. 21c) and 12.5 mm

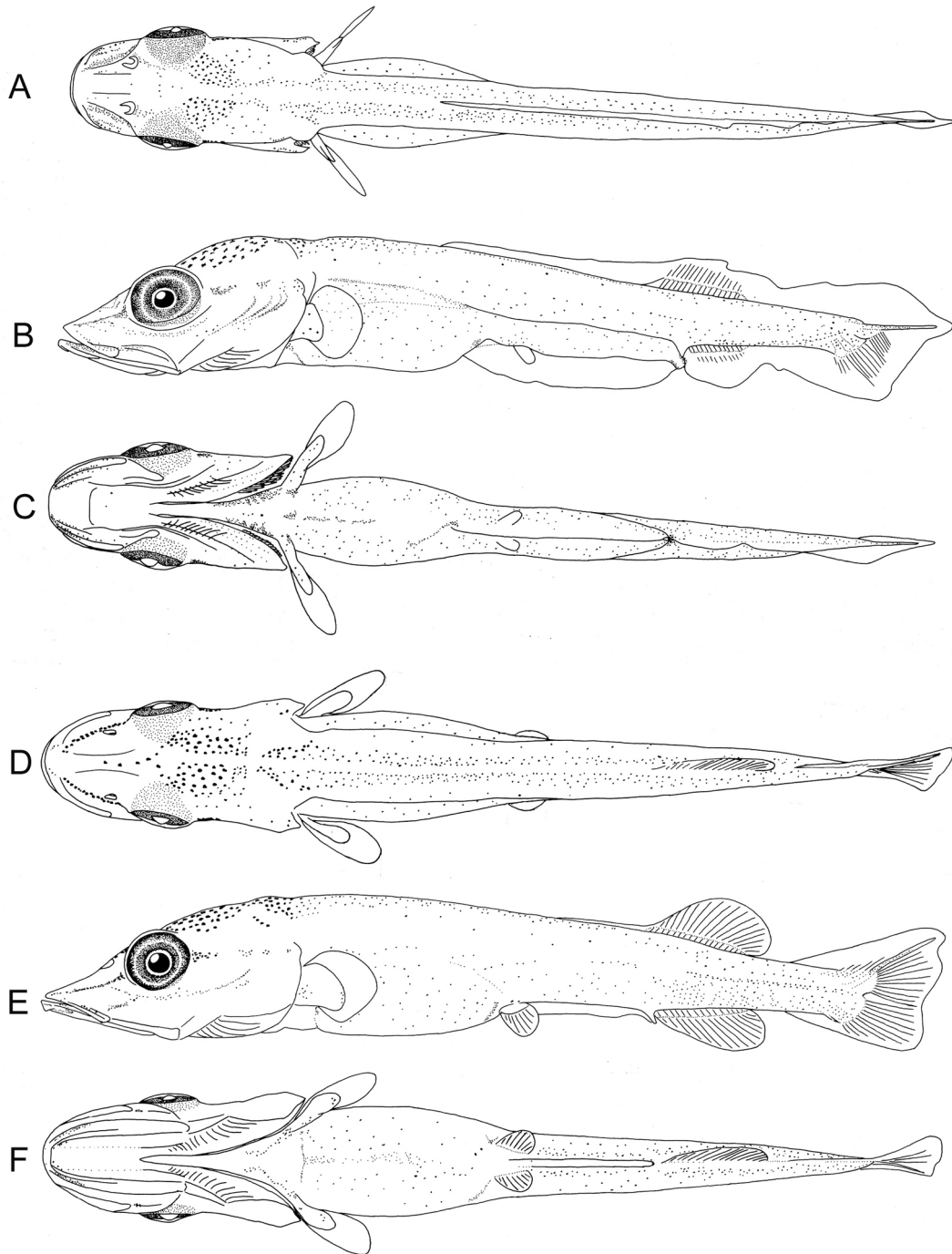


FIGURE 15.—Dorsal, lateral, and ventral views of a 16.5 mm Northern Pike larva (A to C); and dorsal, lateral, and ventral views of a 22 mm Northern Pike larva (D to F), both from Garlock Bay.

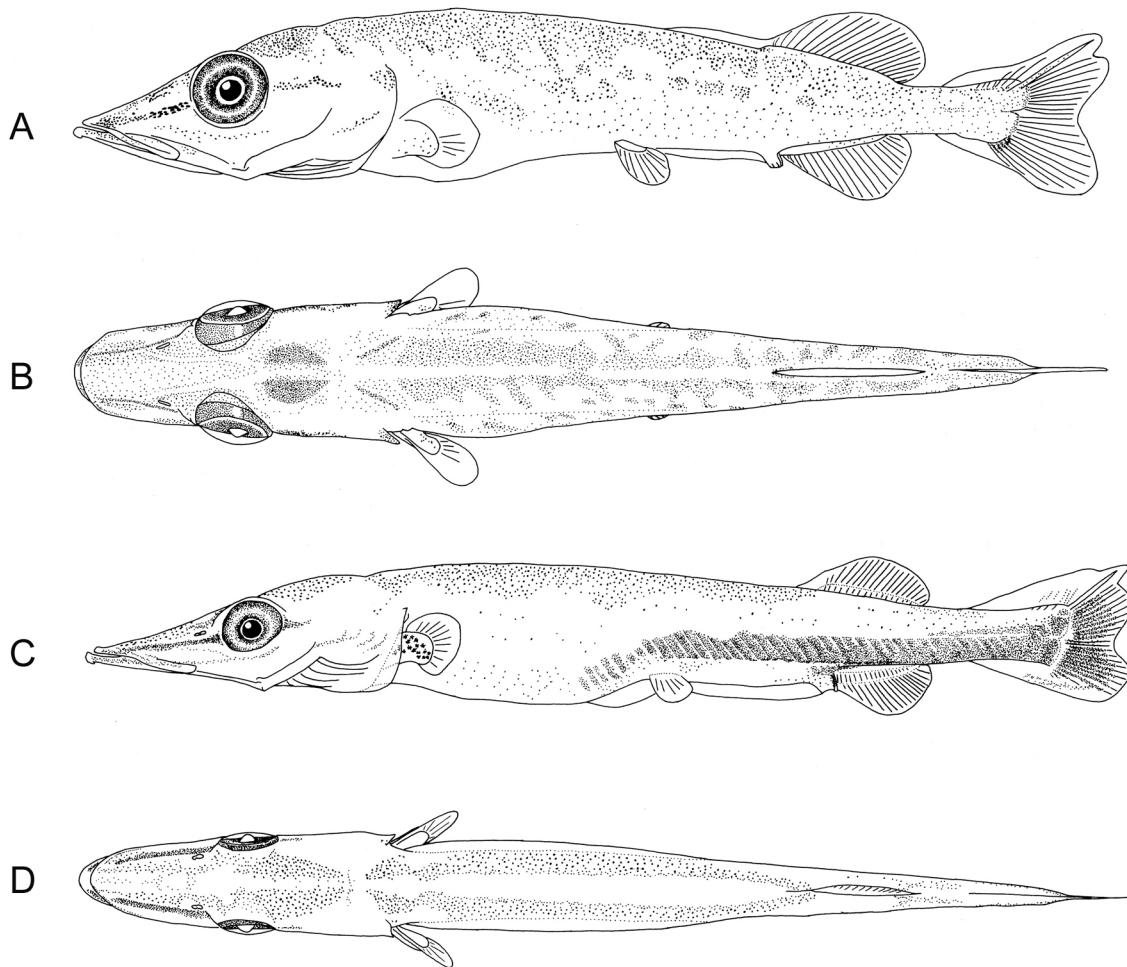


FIGURE 16.—Lateral and dorsal views of a 30 mm Northern Pike larva (A and B, Garlock Bay), and a 30.5 mm Muskellunge larva (C and D, Blind Bay).

Muskellunge (Fig. 22c) which resulted in three patterns of folding in Northern Pike but only two in Muskellunge. Longitudinal folds that covered the stomach became shortened and oriented across the intestine at about halfway along the tract in Northern Pike but continued longitudinally to the first sphincter in Muskellunge. Another sphincter formed halfway along the gut in Northern Pike where the folding pattern changed. The urinary bladder was well formed and was located on the dorsal surface of the intestine. Differentiation in 14 mm Northern Pike consisted of elaboration of the folding in the last two sections of the intestine, the initial formation of a loop in the middle intestine, the emergence of the spleen and gall bladder, and the thickening of the stomach wall which reduced the visibility of the folding. The gas bladder had enlarged and occupied a depression in the dorsal surface of the stomach (Fig. 21d). A second sphincter had formed near the midpoint of the gut in 15 mm Muskellunge, and the mucosal

folding had formed into a third pattern (Fig. 22d), which separated the Muskellunge gut into three sections similar to that in Northern Pike. Enlargement of the gas bladder and the emergence of the spleen occurred at 15 mm in Muskellunge. The middle intestinal loop extended forward toward the frontal lobe of the liver in 20 mm Northern Pike and the spleen had become repositioned at the posterior end of the stomach. The urinary bladder had moved to a depression in the left side of the intestine (Fig. 21e). A median septum had formed in the gas bladder. The mid-intestinal loop formed in Muskellunge larvae at 25 mm along with the emergence of the gall bladder and repositioning of the spleen (Fig. 22e). The gross morphology of the gut in 34 mm Muskellunge (Fig. 22f) was similar to that in 20 mm Northern Pike.

Sensory pores.—Three submandibular pores were present in 14–15 mm Northern Pike and Muskellunge, five pores

Northern Pike and Muskellunge development, growth, and food

TABLE 3.—Total length (TL) and degree days (DD; post-fertilization) required to reach specific events in Northern Pike and Muskellunge raised in 1994.

Character	Northern pike				Muskellunge	
	Garlock Bay		Deer Island Bay		Blind Bay	
	TL (mm)	DD	TL (mm)	DD	TL (mm)	DD
Mouth open	8	124	9	124	10	187
Gill arch filaments	10	172	10	172	10	187
Swim-up	11	216	12	205	13	252
Exogenous feeding	11	239	12	226	14	300
Pelvic fin buds	11	251	12	226	15	370
Caudal fin incipient rays	11	251	12	211	15	317
Yolk absorbed	11	275	12	226	15	317
Tongue teeth	14	288	14	239	14	300
Dorsal/anal fin anlagen	14	301	14	260	16	331
Epural and hypural anlagen	14	301	14	391	16	331
Uprturned urostyle	22	562	22	478	20	430
Epihyal rays	8 rays @ 22	562	8 rays @ 22	478	10 rays @ 27	740
Ceratohyal rays	7 rays @ 27	678	7 rays @ 27	562	8 rays @ 29	770
Dorsal, anal finrays complete	30	751	30	645	30	865

were present in 27 mm Northern Pike, and nine pores were present in 50 mm Muskellunge. The supraorbital canal was represented by two pairs of pores anterior to the eyes in 14–15 mm Northern Pike and Muskellunge. Four pores in the infraorbital canal were present in Northern Pike and Muskellunge at 19 mm. The first pores of the preopercular canal were present in 27 mm Northern Pike and in 30 mm Muskellunge.

Exogenous feeding and behavior.—Exogenous feeding began at 13 mm in Northern Pike at 226 DD and 239 DD (11–13 days post-hatching), and at 300 DD (11 days post-hatching) in Muskellunge. The majority of both species exhibited a lie-and-wait strategy of predation and would strike at brine shrimp that were 3–5 mm away. Some fish would cruise short distances (5–6 body lengths) before making a strike at a prey shrimp. Fish would generally flex their tail in an S-shape just prior to striking but would also strike without showing this behavior. The S-shape behavior was also observed when no strikes at prey were made and

may have been a means to reposition the fish. Many strikes were unsuccessful and the missed prey was rarely pursued: fish would more often select a different prey. Prey were generally taken either in the same plane as the predator or at a lower elevation. There were exceptions to this as some fish would swim upward in pursuit of prey. Northern Pike and Muskellunge would frequently swim backward after a strike, effectively reaching their original starting position. Both species avoided most "face-to-face" encounters but when encounters occurred, the smaller of the fish would move away. Fish were generally spaced two to three body lengths from their closest neighbor and would occupy positions in the entire water column. Some fish would face downward at 30° to 70° from horizontal for several minutes. This was more prevalent in Muskellunge.

Isometric and allometric growth.—Five body structures were measured for isometric and allometric growth in fish

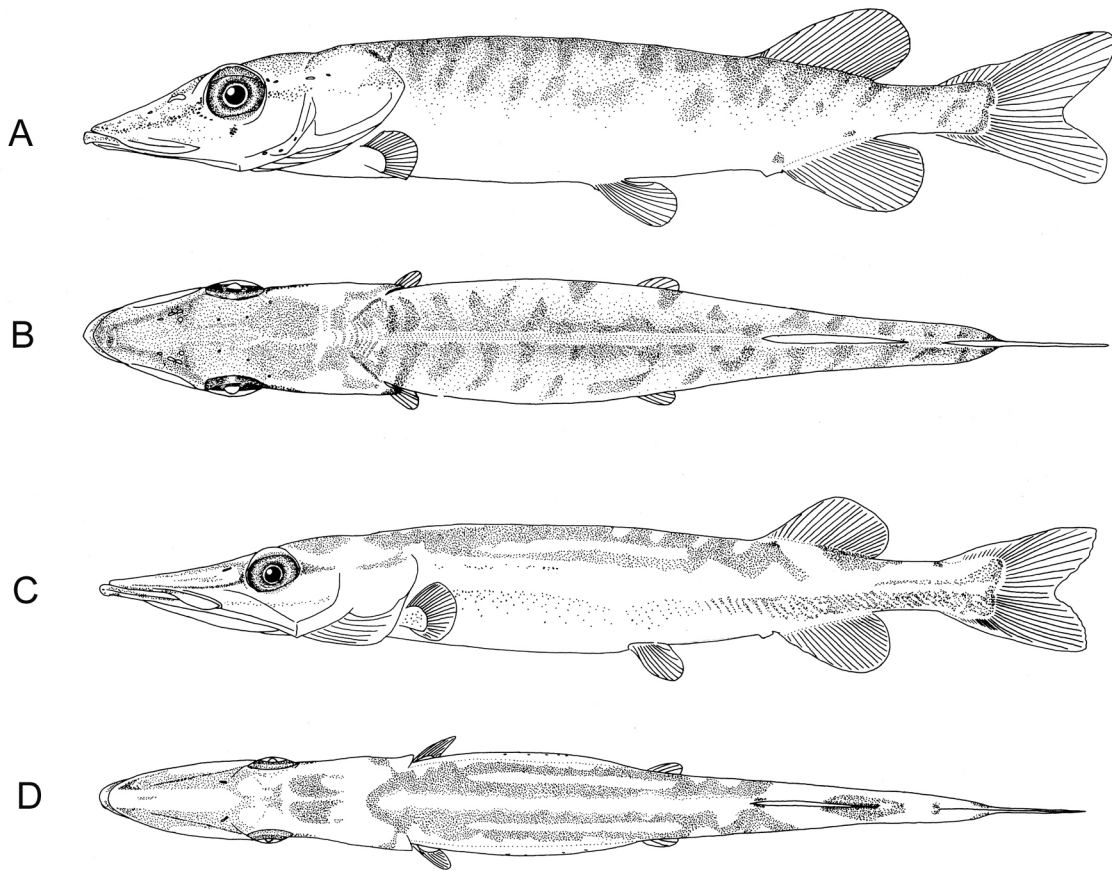


FIGURE 17.—Lateral and dorsal views of a 54 mm Northern Pike juvenile (A and B, Garlock Bay), and a 54 mm Muskellunge juvenile (C and D, Blind Bay).



FIGURE 18. Lateral body pigmentation of Muskellunge juveniles showing the characteristic spots of the Great Lakes strain. Fish total lengths, from top, are 124 mm, 130 mm, and 122 mm.

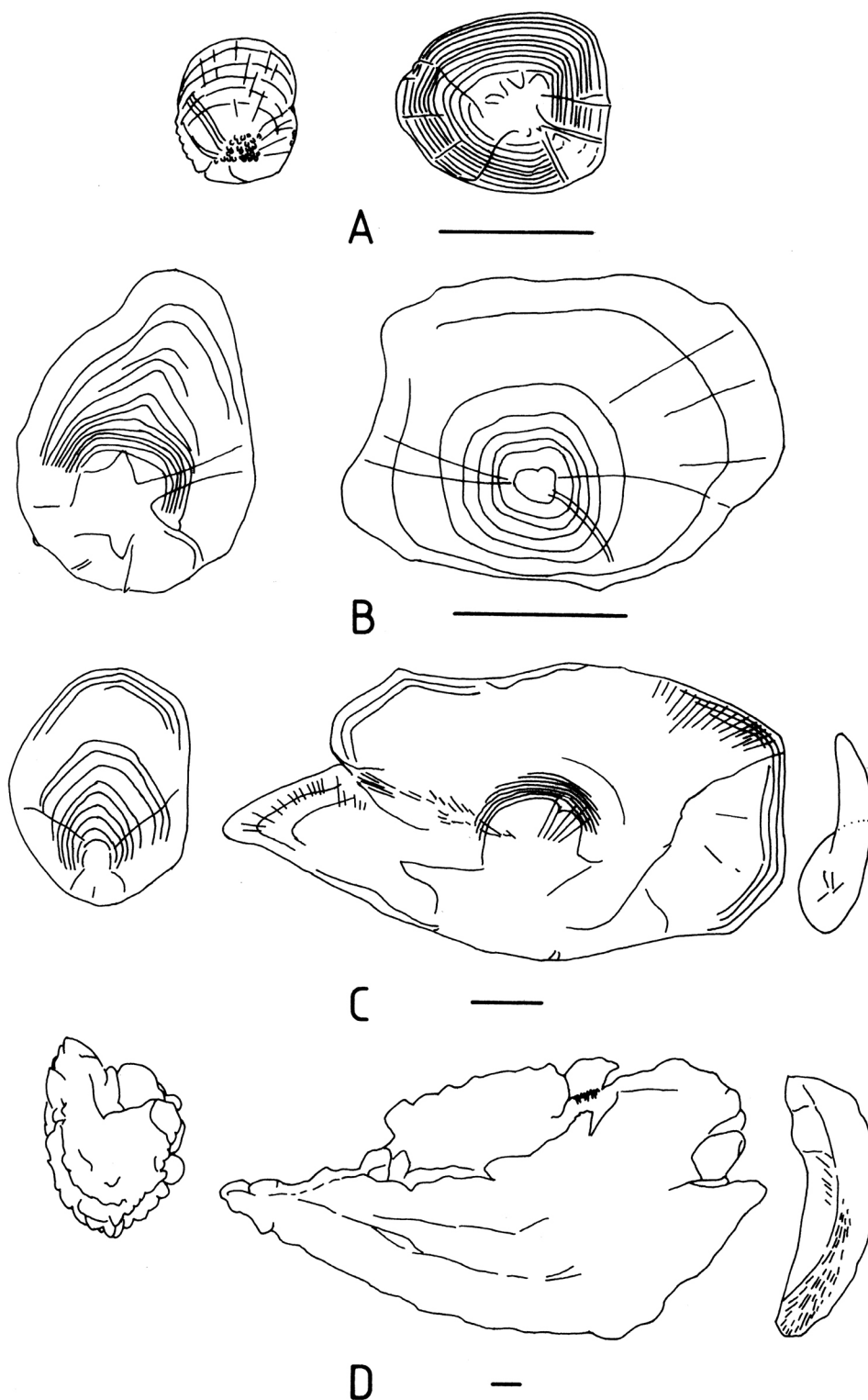


FIGURE 19.—Otoliths from the left side of Northern Pike A) lapillus (left) and sagitta (right) from 14.5 mm larva; B) lapillus and sagitta from 22.5 mm larva; C) lapillus, sagitta and asteriscus from 47 mm larva; and D) lapillus, sagitta, and asteriscus from 122 mm juvenile. The sulcus is not visible in these views. Scale bars equal 0.1 mm.

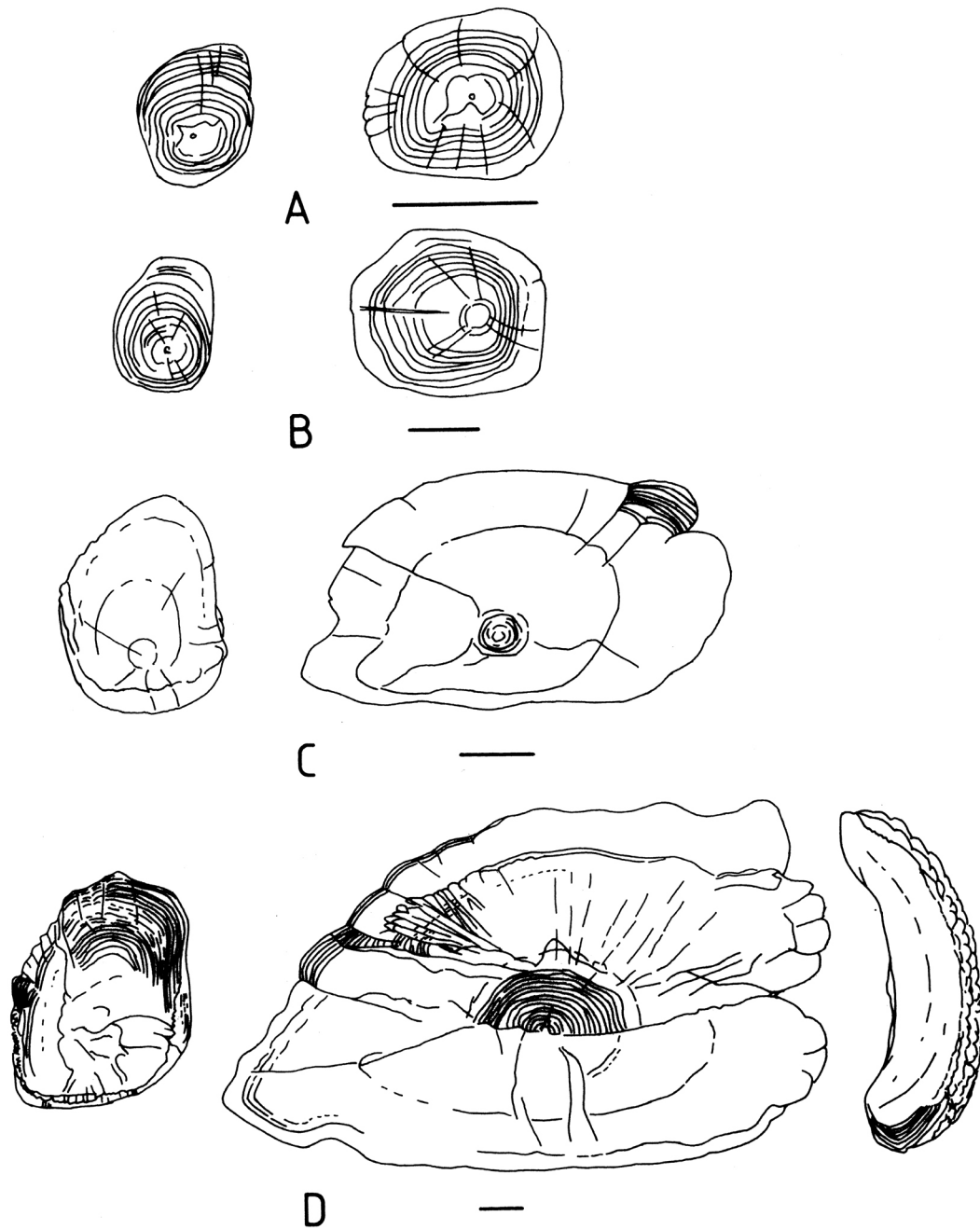


FIGURE 20.—Otoliths from the left side of developing Muskellunge larvae A) lapillus (left) and sagitta (right) from a 14 mm larva; B) lapillus and sagitta from a 28 mm larva; C) lapillus and sagitta from a 50 mm larva; and D) lapillus, sagitta, and asteriscus from a 122 mm juvenile. The sulcus is not visible in these views. Scale bars equal 0.1 mm.

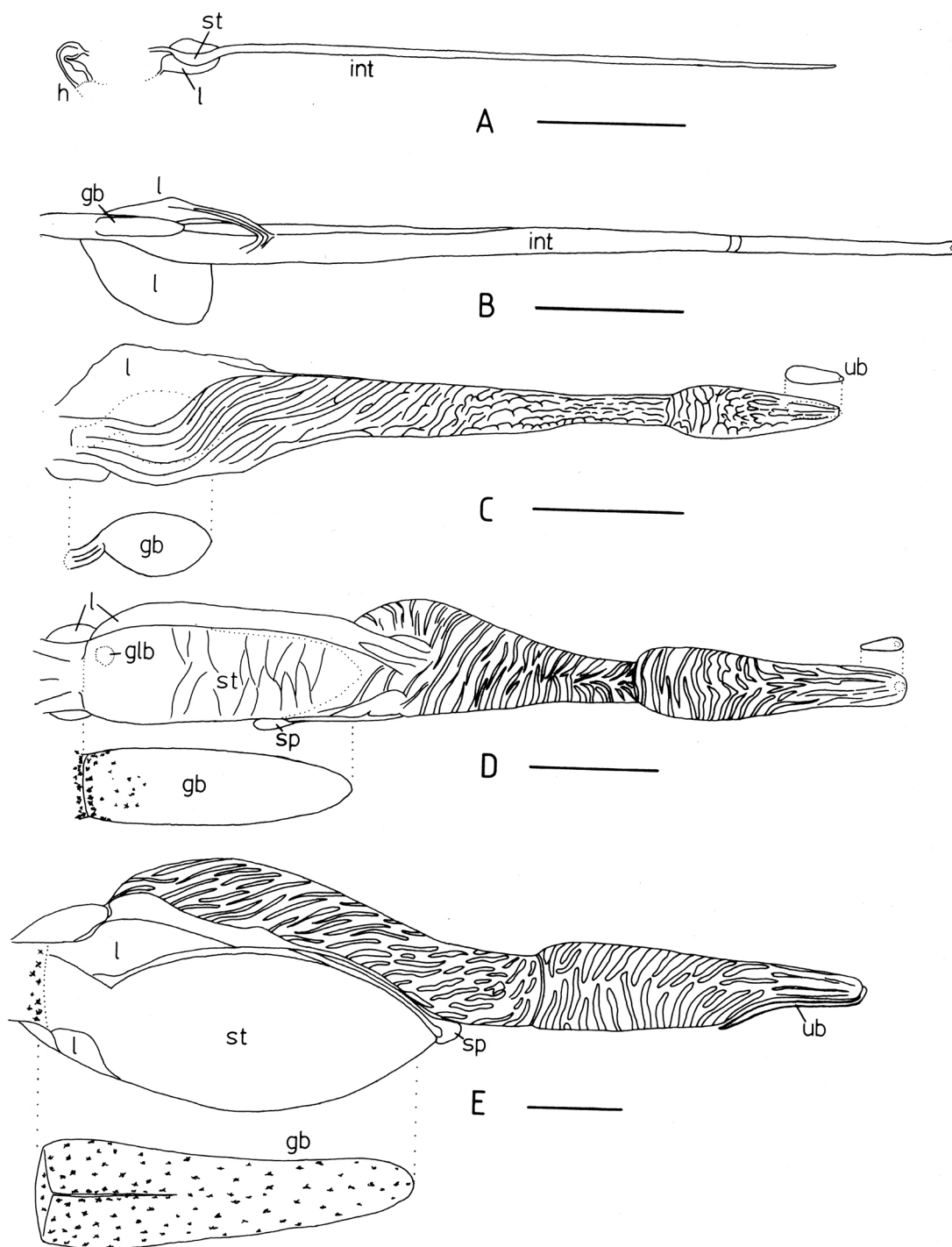


FIGURE 21.—Dorsal views of gross development of the alimentary tract in Northern Pike larvae from Garlock Bay. Gas bladder and urinary bladder have been moved laterally in some views (shown by stippling). Total length of Northern Pike: A) 8.4 mm; B) 10.4 mm; C) 11.8 mm; D) 14 mm; E) 20 mm. Key to structures: glb—gall bladder, gb—gas bladder, h—heart, int—intestine, l—liver, sp—spleen, st—stomach, ub—urinary bladder. Scale bar equals 1mm.

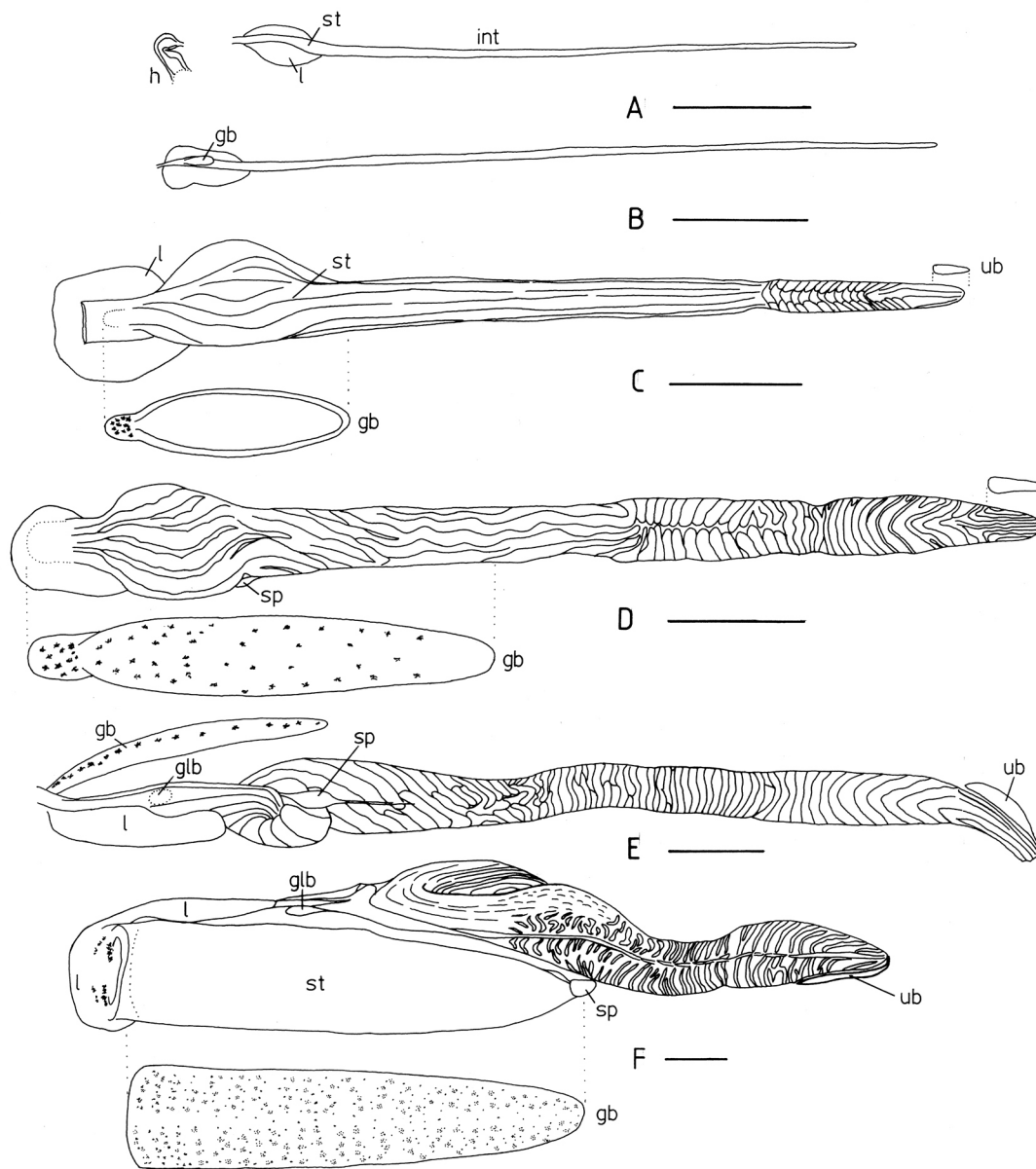


FIGURE 22.—Dorsal views (A–D and F) of the gross development of the alimentary tract and lateral view (E) in Muskellunge larvae from Blind Bay. Gas bladder and urinary bladder have been moved laterally in some views (shown by stippling). Total length of Muskellunge: A) 8.2 mm; B) 10.2 mm; C) 12.5 mm; D) 15 mm; E) 25 mm, F) 34 mm. Key to structures: glb—gall bladder, gb—gas bladder, h—heart, int—intestine, l—liver, sp—spleen, st—stomach, ub—urinary bladder. Scale bar equals 1 mm.

raised in 1994, and 1996–1998 (Fig. 23). Only preanal length was found to show isometric changes. Snout length (SnL) showed the greatest changes which occurred primarily between fish lengths of 10–15 mm. There were at least two growth stanzas in each of the body structures with allometric growth and perhaps three growth stanzas in SnL. The growth patterns were similar between Northern Pike and Muskellunge; only SnL differed appreciably reaching a

greater length in Muskellunge. Measurements of all body structures are summarized in appendix Table 1.

Water temperature for the feeding experiments differed by as much as 7°C from late May to the third week of June (Fig. 24). Water temperature remained colder for a longer period in 1996 in the laboratory and in the bays from which fish were collected, reflected by the later start of feeding for Muskellunge.

Northern Pike and Muskellunge development, growth, and food

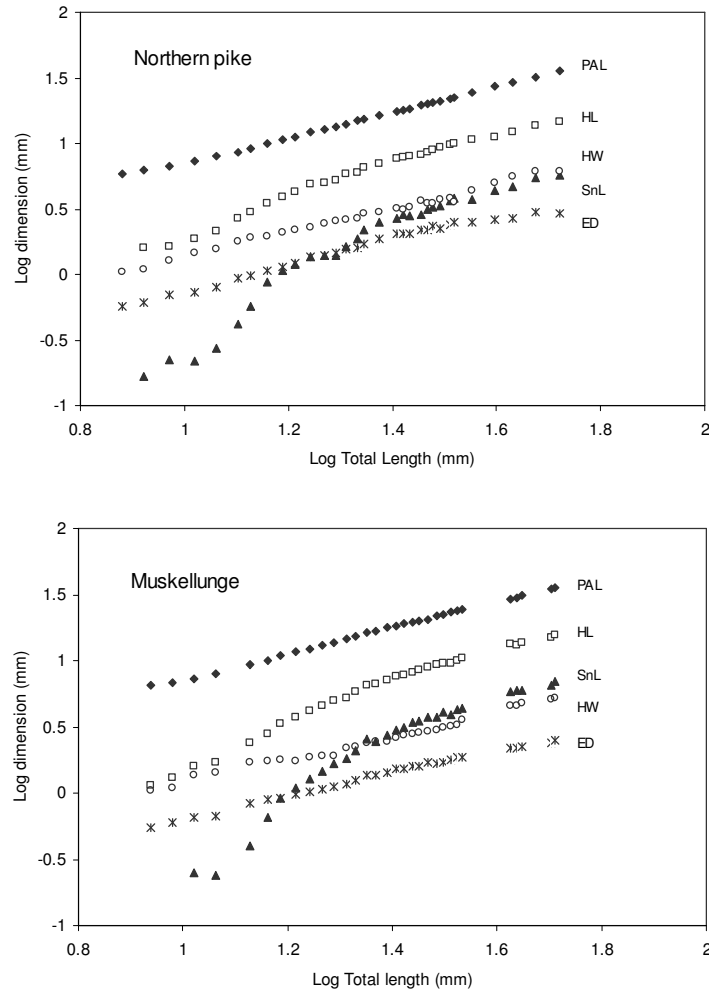


FIGURE 23.—Comparison of TL and growth of body structures in Northern Pike and Muskellunge larvae. A straight line represents isometric growth. Morphology abbreviations are ED—eye diameter, HL—head length, HW—head width, PAL—pre-anal length, and SnL—snout length. N=266 fish for each species.

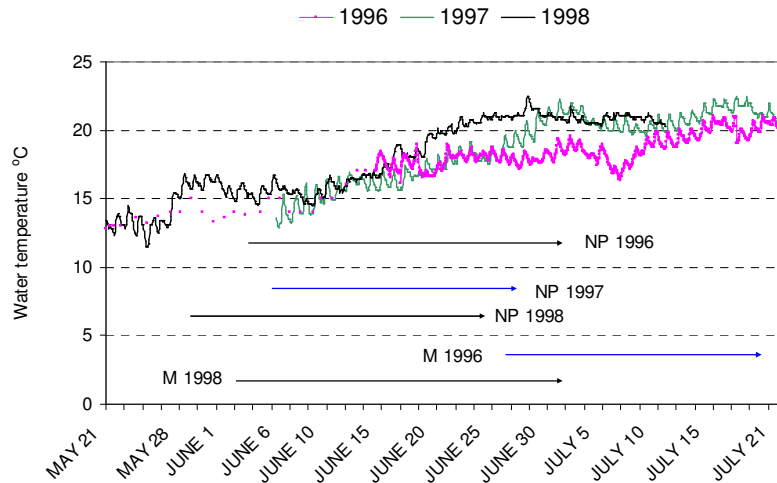


FIGURE 24.—Water temperature profiles for the feeding periods for Northern Pike and Muskellunge in the laboratory experiments. The length of each arrow indicates the feeding period and the line colors show the diet: black for a brine shrimp diet and blue for comparisons of two diets: brine shrimp and fish larvae.

Regressions of mean weight against mean TL resulted in significantly different estimates of Northern Pike growth in 1996, 1997, and 1998, but not for Muskellunge (Fig. 25). Regressions of mean weight and age, and mean weight and DD, resulted in significantly different estimates for Northern Pike and Muskellunge. Linear regressions of TL and age for both years overestimated the weight of Northern Pike between 18–26 mm, and underestimated the weight of Northern Pike longer than 31 mm. Linear regressions overestimated the weight of Muskellunge between 17–24 mm and overestimated the weight of 15–27 day-old Muskellunge. Examination of the residuals from ANOVA indicated that quadratic equations, and power functions, would reduce the residuals, and thus describe the relationships better than linear regressions. Quadratic

equations represented a better fit to the data than power functions for Northern Pike weight by age in 1996, Muskellunge weight by TL in 1998, and Muskellunge weight by age in 1998. Power functions are listed to the left of the relationships in Fig. 25, and quadratic equations are given in Table 4.

The instantaneous rate of growth in TL and weight was greater in 1998 than in 1996. Daily increases in length were also greater in 1998 than in 1996 but daily increases in weight were the same. Instantaneous growth rate in weight was greater in 1996 than in 1998 but the instantaneous rate in TL was the same. Daily increases in weight and TL were greater in 1996 than in 1998 (Table 5).

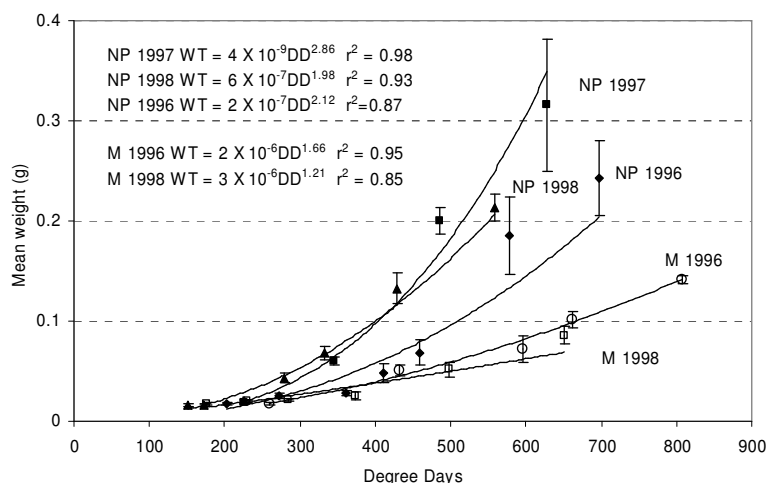


FIGURE 25.—The relationship of mean weight (g) to degree days for Northern Pike and Muskellunge raised on brine shrimp. Data points are mean weight: Northern Pike, solid square, 1997; Northern Pike, solid triangle, 1998; northern Pike, solid diamond, 1996; Muskellunge, open circle, 1996; and Muskellunge, open square, 1998. Bars represent one SE.

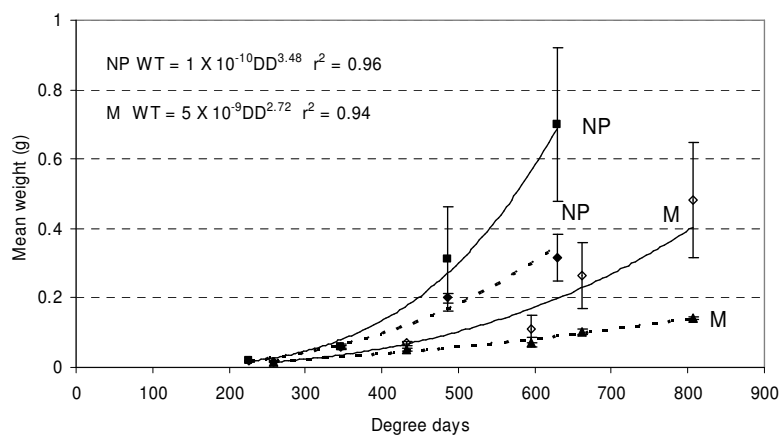


FIGURE 26.—Comparison of the mean weight (g) to degree day (DD) relationship for Northern Pike (1997) and Muskellunge (1996) on two diets: solid lines represent a fish larvae diet and dotted lines represent a brine shrimp diet. Growth equations for the fish diet are shown in this graph while growth equations for the shrimp diet are shown in Fig. 25. Bars equal one standard error.

Northern Pike and Muskellunge development, growth, and food

TABLE 4.—Quadratic equations describing the relationship of TL, age, and DD to WT for Northern Pike and Muskellunge raised on brine shrimp. Durbin-Watson values near 2.0 indicate that there was no autocorrelation between the variables. DW near 0 for pike in 1997 would suggest positive autocorrelation.

Northern pike				
Year	Equation	r ² value	Sample size for year	Durbin-Watson value
1996	WT = 0.06–0.009TL + 0.0005TL ²	0.98	75	2.0
1996	WT = 0.04–0.006AGE + 0.0003AGE ²	0.90		1.4
1996	WT = 0.074–0.0005DD + 0.000001DD ²	0.90		1.4
1997	WT = -0.03+0.001TL + 0.0002TL ²	0.98	30	1.1
1997	WT = 0.03–0.0076AGE + 0.00036AGE ²	0.95		0.9
1997	WT = 0.03–0.0004DD + 0.000001DD ²	0.95		0.8
1998	WT = 0.005–0.002TL + 0.0002TL ²	0.98	40	1.5
1998	WT = 0.015–0.002AGE + 0.0003AGE ²	0.98		2.5
1998	WT = 0.012–0.0001DD + 0.0000008DD ²	0.98		2.0

Muskellunge				
Year	Equation	r ² value	Sample size for year	Durbin-Watson value
1996	WT = -0.009 + 0.0006TL + 0.0001TL ²	0.98	35	1.9
1996	WT = -0.0006 + 0.002AGE + 0.00003AGE ²	0.96		2.0
1996	WT = -0.168 + 0.0001DD + 0.0000001DD ²	0.98		1.3
1998	WT = 0.092–0.010TL + 0.0004TL ²	0.96	35	2.2
1998	WT = 0.02–0.001AGE + 0.00009AGE ²	0.95		2.0
1998	WT = 0.028–0.0001DD + 0.0000003DD ²	0.95		1.2

TABLE 5.—Instantaneous and daily increases in total length (TL, mm) and weight (WT, g) for Northern Pike and Muskellunge raised on a brine shrimp diet.

Northern pike						
	1996		1997		1998	
	TL	WT	TL	WT	TL	WT
Instantaneous increase (G)	0.03	0.005	0.05	0.13	0.04	0.10
Daily increase	0.61	0.007	1.17	0.10	0.92	0.007

Muskellunge					
	1996		none raised in 1997	1998	
	TL	WT		TL	WT
Instantaneous increase (G)	0.03	0.07		0.03	0.05
Daily increase	0.67	0.003		0.50	0.002

Objective 2.—Growth of Northern Pike and Muskellunge larvae on different diets. Both species started feeding on a first food of fish larvae at 8 d after hatching at 13 mm and could consume prey fish up to 66% of predator TL. Northern Pike consumed 6–12 mm Yellow Perch (*Perca flavescens*) and 5–12 mm Golden Shiner (*Notemigonus crysoleucas*) but not Smallmouth Bass (*Micropterus dolomieu*) or Largemouth Bass (*M. salmoides*) at 6–8 mm.

Larger predators consumed the longer prey. Smallmouth and Largemouth Bass have larger cross-sectional areas than the consumed species (Fig. 27) and may have appeared too large to attack. Brook Silverside (*Labidesthes sicculus*) larvae were not presented to Northern Pike because silverside were not seen when Northern Pike began to feed in the wild.

Muskellunge consumed 7–8 mm Carp (*Cyprinus carpio*), 6–13 mm Spottail Shiner (*Notropis hudsonius*), and

5–12 mm Golden Shiner but not 7–15 mm Brook Silverside. When shiners and silverside were presented together, only the shiners were eaten. Silverside would be attacked but quickly spit out when they were the only prey. Silverside have a similar shape to the other prey fish (Fig. 27) which would suggest that the factor causing rejection may have been taste or texture. Some silverside became lodged in the Muskellunge throats and the Muskellunge died. Northern Pike have a larger gape and vertical height of the mouth than Muskellunge, which resulted in a greater cross-sectional area at all fish lengths measured. Growth in weight of Muskellunge and Northern Pike was faster on fish larvae than on brine shrimp (Fig. 25). Muskellunge feeding on brine shrimp did not show any change in growth rate but the growth rate of Muskellunge feeding on fish larvae increased from 0.004g/day to 0.03g/day at 26 days after

hatching. Northern Pike showed a growth rate increase at 26 days after hatching on both diets: from 0.006g/day to 0.017g/day on brine shrimp; and from 0.005g/day to 0.043g/day on fish larvae. Water temperature did not increase as rapidly during Muskellunge incubation in 1996 as it did during Northern Pike incubation in 1997 and may have retarded Muskellunge growth to some extent (Fig. 25). The comparisons between the brine shrimp diet and fish larvae diet for each species within years would not be affected by these water temperature differences. The presence or activity of digestive enzymes was not determined but may have lagged behind the development of the gut since many prey fish were identifiable to species after having passed through the digestive system. Prey fish remained recognizable for a longer time in Muskellunge than in Northern Pike.

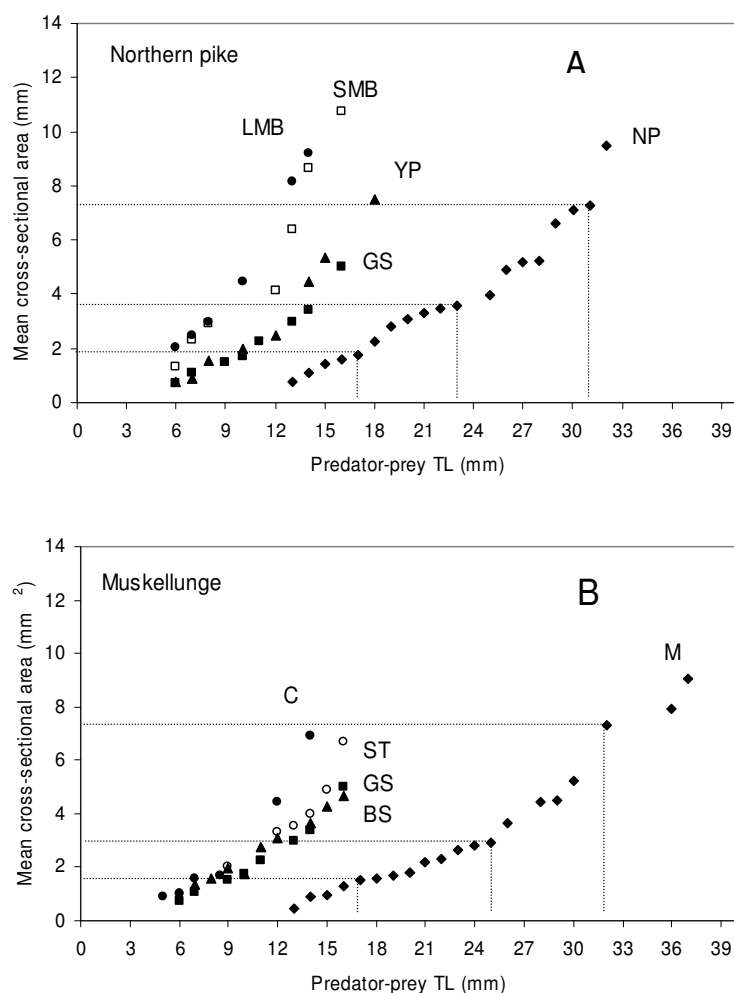


FIGURE 25.—Relationship between the mouth cross-sectional area of Northern Pike and Muskellunge and the body cross-sectional area of prey species of fish larvae. Mouth cross-sectional area is the product of gape multiplied by height. Each symbol represents the mean of larvae within a 1 mm length increment. Key to prey fish for *Northern Pike* (A): LMB—Largemouth Bass (solid circle), SMB—Smallmouth Bass (open square), YP—Yellow Perch (solid triangle), and GS—Golden Shiner (solid square); for *Muskellunge* (B) C—Carp (solid circles), ST—Spottail Shiner (open circle), GS—Golden Shiner (solid square), and BS—Brook Silverside (solid triangle). Gape for Northern Pike (NP) and Muskellunge (M) are shown as black diamonds.

Cannibalism was present in Northern Pike at an equivalent fish density of 266/m² but was observed in Muskellunge only at equivalent densities greater than 11,000/m². Cannibalism started in both species at 19 mm between 20–21 days after hatching. The length ratio between predator and prey was 1.2:1 for both species. Cannibals were removed from the experiments and were not used in the regressions. Northern Pike raised (at equivalent fish density of 14,000/m²) on brine shrimp in 1996 for a separate experiment had diverged into two groups after 51 days of age. A subsample of one group (n=39) that was fed only brine shrimp had a mean TL of 39 mm (SD=2.87) and a mean weight of 0.207 g (SD=0.05) while a subsample of their cannibalistic siblings (n=39) had reached a mean TL of 66 mm (SD=7.4) and a mean weight of 1.31g (SD=0.56). Instantaneous rate of growth in weight in Northern Pike

cannibals (0.056g) was 37 times greater than in the non-cannibal Northern Pike (0.0015g) and 3.8 times as great in growth in length (cannibals 1.88 mm; non-cannibals 0.5 mm).

Wild fish diets.—The diets of wild Northern Pike and Muskellunge larvae were examined to determine if either species fed on prey fish at a similar size as in the artificial feeding trials. Twenty-eight percent of Muskellunge 16–18 mm in length (n=7) had fed on fish larvae and 75% of Muskellunge between 18.5–25 mm (n=23) had fed on fish larvae. Northern Pike that were less than 23 mm in length did not feed on fish larvae and only 14% of Northern Pike between 23–28 mm in length (n=7) had fed on fish larvae. The shortest Muskellunge that fed on fish larvae was 16.5 mm. The diets of all fish examined are summarized in Table 7.

TABLE 7.—Mean number of prey items per fish consumed by wild Northern Pike and Muskellunge by size class (TL) collected in 1992 and from 1996–1998.

Prey taxa	Northern pike		Muskellunge	
	15–20 mm (N=11)	21–28 mm (N=11)	16–20 mm (N=15)	21–28 mm (N=14)
Cladoceran	8.5	16.9	4.6	2.9
Copepod	10.1	7.3	2.8	0
Midge larvae	1.4	1.5	0.8	0
Golden shiner	0	0	0.4	0.4
Carp	0	0	0.1	0.1
Unidentified fish	0	0.1	0.4	0.1
Ostracod	1.1	0.2	0	0
Amphipod	0	0.2	0	0
Phantom midge	0	0.1	0	0
Biting midge	0	0.1	0	0
Mayfly	0	0.1	0	0
Rotifer	0	0	0.1	0.1

Discussion

Gross development.—Morphological development of Northern Pike and Muskellunge eggs and larvae were similar and shared several characteristics: a continuous finfold, adhesive eggs and adhesive papillae, large yolk, rate of yolk utilization, and limited pigmentation on the margins of the eyes at hatching. The range of egg diameters for Northern Pike in the present study were similar to that in Franklin and Smith (1963) and Farrell (1996), larger than that in Clark (1950) and Leslie and Gorrie (1985), but smaller than the mean diameter in Buynak and Mohr (1979). The range of egg diameters in Muskellunge in the present study was similar to that in Leslie and Gorrie

(1985), Fish (1932), and to the mean in Buynak and Mohr (1979) but smaller than that in Farrell et al. (1996). Hatching lengths of Northern Pike are similar in North America (Franklin and Smith 1963; Buynak and Mohr 1979; Leslie and Gorrie 1985; present study) and in Europe (Frost and Kipling 1967; Kotylarevskaya 1969). Mean hatching lengths in Muskellunge are generally larger than in Northern Pike but there is overlap in the ranges. The range of Muskellunge hatching lengths in the present study were within those found by Leslie and Gorrie (1985) and Buynak and Mohr (1979).

Development was faster in Northern Pike than in Muskellunge in variable water temperatures (this study) and controlled water temperatures (Cooper et al. 2008) and

would support the idea that Northern Pike are more tolerant of colder water. The time required to reach specific developmental characteristics in the present study was similar to that reported for Northern Pike (Frost and Kipling 1967; Franklin and Smith 1963; Buynak and Mohr 1979) and for Muskellunge (Galat 1973) with the exception of the presence of a developing mouth described by Galat as a visible line in 12 day-old embryos. The mouth line was not seen in Muskellunge in this study until after hatching.

The presence of oil globules in the eggs of Northern Pike has been previously noted by Fish (1932) but were not seen by Franklin and Smith (1963) at the time of egg deposition. Oil globules were present in unfertilized and fertilized Northern Pike and Muskellunge eggs in the present study. The movement of the oil globules during embryogenesis of both species was similar to the description given by Galat (1973) for Muskellunge and to that for Redfin Pickerel *Esox americanus* by Malloy and Martin (1981). Oil globules were scattered throughout the yolk in Northern Pike and Muskellunge larvae unlike the aggregation of oil globules at the anterior part of the yolk in Redfin Pickerel (Malloy and Martin 1981).

The two species differed primarily in pigmentation patterns and density of melanophores. The yolk sacs of Northern Pike larvae were more densely pigmented than those in Muskellunge, and Muskellunge had denser pigmentation along the hypaxial tissue of the body. These differences were present in most of the developmental period examined in this study.

Coordination of developmental characters was most evident just prior to exogenous feeding. The opening of the mouth coincided with development of the first vomerine teeth, cartilage in the jaws and branchial chamber, and extensive folding in the intestine. These characters would contribute to more efficient feeding. The presence of digestive enzymes in the intestine was not determined but their development may have lagged behind alimentary tract development since much of the food provided was recognizable after passing through the digestive process in laboratory-raised fish. A similar result was noted in Northern Pike larvae by Ivanova and Lopatko (1984) and Morrow et al. (1997). Szlaminska (1980) noted that pepsin and trypsin activity was present in 18-day old Northern Pike larvae but it is not known if this is true for Muskellunge. More complete digestion may result in some fish from the activation of trypsin, obtained from prey fish, by the high pH in the hindgut of the predator (Govoni et al. 1986).

Balon (1975) described the presence of adhesive eggs and adhesive papillae in Esocidae as specific adaptations that would enable the eggs and larvae to attach to vegetation above areas that could have low dissolved oxygen. Numerous studies have reported adhesive eggs for Northern Pike and the presence of adhesive papillae in Northern Pike was noted by Gulidov (1969), Kotylarevskaya (1966), and Frost and Kipling (1967). The more extensive works (Kotylarevskaya 1969; Braum et al. 1996) have examined

the cellular and ultrastructure characteristics of the papillae. Kotylarevskaya (1969) described the behavior exhibited by Northern Pike shortly after hatching that involved the use of the adhesive papillae: 1) an immediate swimming upward to attach, 2) remaining motionless on the substrate, and 3) swimming upward to attach but also swimming about at irregular intervals and reattaching. These three types form a gradient that can encompass the various behaviors attributed to Northern Pike (Hiner 1961; Franklin and Smith 1963; Dombeck et al. 1984; Braum et al. 1996), to Muskellunge (behavior #2 only; Dombeck et al. 1984), and Chain Pickerel (*E. niger*; Underhill 1949), although Chain Pickerel attached only at night in aquaria. Northern Pike and Muskellunge exhibited similar behavior in the present study: motionless on the substrate immediately after hatching with increasing periods of movement until they became attached above the substrate 3–4 d after hatching.

Muskellunge have been attributed with lacking adhesive eggs (Scott and Crossman 1973; Dombeck et al. 1986) and having larvae that do not exhibit vegetation attachment behavior (Dombeck et al. 1984), thus being unique in the pike family. Cooper (1983), however, reported that Muskellunge do have adhesive eggs and Sorenson et al. (1966) reported that Northern Pike and Muskellunge eggs lose their adhesiveness after water hardening, as does the Chain Pickerel (Underhill 1949). Muskellunge eggs were adhesive in the present study but lost that adhesiveness after water hardening. This observation was supported by the collection of wild-caught Northern Pike and Muskellunge water-hardened eggs, which were nonadhesive in the present study and in Farrell et al. (1996). Muskellunge larvae exhibited the attachment behavior in rearing tanks in the present study and in studies by Sorenson et al. (1966) and Colesante (1977). Papillae were detectable in Muskellunge larvae up to 14.5 mm (Leslie and Gorrie 1985), similar to that found in the present study. The hypothesis that Muskellunge do not exhibit the attachment behavior can be rejected. These results show that Muskellunge are similar to the other members of the Esocidae in this adaptation to potentially low-oxygen environments.

Another adaptation described by Balon was a dense network of blood capillaries found on the yolk, and this capillary network was illustrated for the Amur Pike *E. reicherti*, endemic to Siberia. This network of capillaries is quite similar to that found in Northern Pike (Kotylarevskaya 1969; present study), Muskellunge (Galat 1973; present study), and Redfin Pickerel (Malloy and Martin 1981). This dense network serves as a respiratory organ until the gills have formed (Balon 1975). The location of the heart is also similar among the Amur Pike (Balon 1975), Redfin Pickerel (Malloy and Martin 1981), Northern Pike and Muskellunge: to the left of the head and lying on the yolk sac at hatching.

The faster growth shown by Northern Pike in 1998 and Muskellunge in 1996 on the brine shrimp diet may be a result of differing temperatures (Fig. 22). Northern Pike

grew faster in the warmer water in 1998 which was closer to their optimal temperature range of 21–26°C (Hokanson et al. 1973). The reverse was true for Muskellunge in 1998, which experienced rapidly increasing water temperatures soon after swim-up, a developmental period where temperature tolerance is reduced (Hassan and Spotila 1975). Northern Pike grew faster than Muskellunge in both years reaching a 57% greater weight at 31 days after hatching.

Growth of Northern Pike and Muskellunge larvae was faster on fish larvae than on brine shrimp and growth of Northern Pike larvae was faster than that of Muskellunge larvae. The capture of fish larvae would represent a greater return in energy for the effort expended than would capturing brine shrimp. The rapid increase in growth rate of Northern Pike and Muskellunge on the fish larvae diet was similar to an increase in juvenile Northern Pike and

Muskellunge described by Hunt and Carbine (1951) and Farrell (1998). Both of these growth rate changes may indicate a major change in the physiological condition of the fish. A comparison of Northern Pike growth (Fig. 28) estimated from logarithmic regressions showed that the Northern Pike raised on fish larvae achieved growth that was similar to that of wild fish (Franklin and Smith 1963; Fago 1977; and LaPan 1985). Northern Pike raised on a diet of zooplankton only (Bry et al. 1995) had a TL–weight relationship that was intermediate to that in Fig. 28. Growth of Muskellunge on the fish larvae diet was similar to that reported by Applegate (1981) for Muskellunge raised on a zooplankton diet (Fig. 29). Cannibalism was present, although limited, in the study by Applegate and may have influenced the recorded growth.

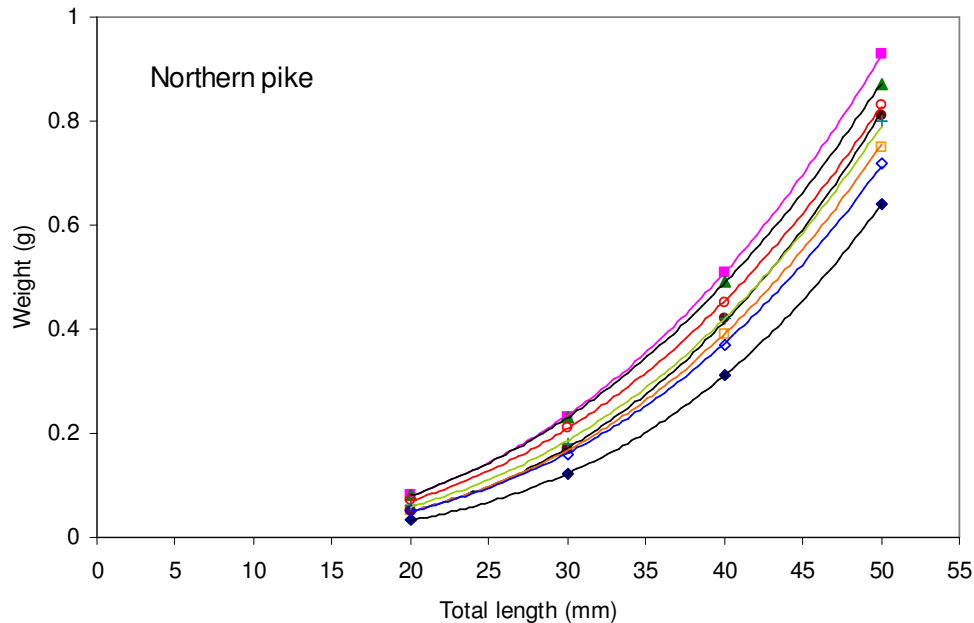


FIGURE 28.—Northern Pike growth curves derived from equations in the following studies starting at the top line at 50 mm: Pleasant Lake Marsh in 1973 (magenta square, Fago 1977); Pabst Marsh in 1972 (black triangle, Fago 1977), 1955 (red circle) and 1957 (black diamond, Franklin and Smith 1963), 1997 (green cross, this study); 1956 (orange square, Franklin and Smith 1963); 1983–1984 (blue diamond, LaPan 1985); and Pleasant Lake Marsh in 1972 (black diamond, Fago 1977). Bry et al. 1995 recorded weights of 0.15g at 27 mm and 0.6g at 46 mm TL.

Cannibalism has been implicated as a major factor in controlling Northern Pike population density (Kipling and Frost 1970) but less is known about the effect of cannibalism in Muskellunge populations. Giles et al. (1986) determined that Northern Pike cannibalism was density-dependent in artificial conditions and this was also true in natural conditions where emigration occurs over a long time (Hunt and Carbine 1951) or where emigration is not possible, as in ponds (Wright and Giles 1987). Cannibalism is less common in areas where emigration time is relatively short, (Franklin and Smith 1963; Morrow et al. 1997). The growth advantage that cannibal Northern Pike have over

their siblings can be dramatic (Giles et al. (1986; present study) and the presence of cannibals may intimidate the smaller Northern Pike to an extent that growth rate is reduced. The cannibal Northern Pike in the present study achieved a similar instantaneous rate of growth to that in Giles et al. (1986) in their own environment. Muskellunge spawn in relatively open bays in the St. Lawrence River (Farrell and Werner 1999), and their larvae may exist at a lower density than Northern Pike larvae spawned in the marshes. Cannibalism did occur under artificial conditions in the present study where density was greater than what would likely be found in nature.

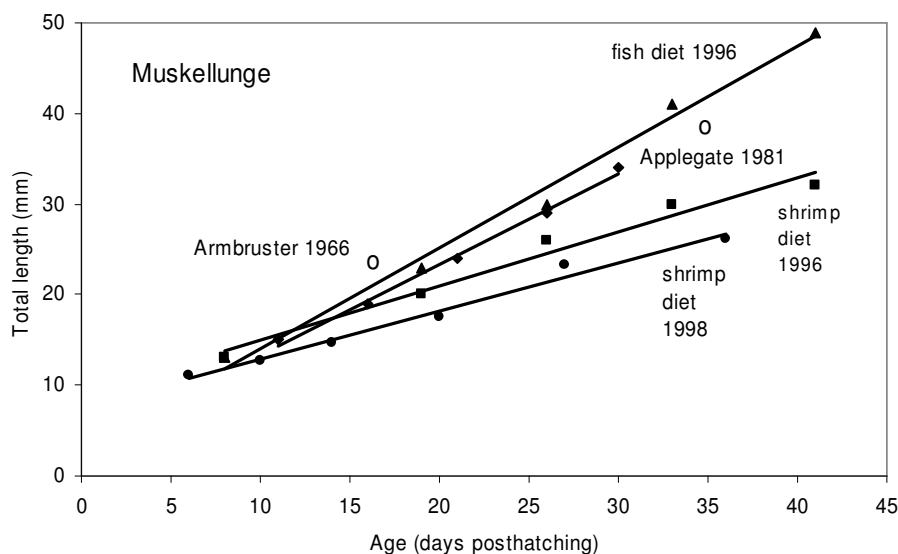


FIGURE 29.—Comparison of increases in TL by age in several studies, from top: this study (green, fish diet), Applegate 1981 (black diamond, mixed diet), this study (magenta, 1996, brine shrimp), and this study (blue circle, brine shrimp, 1998). Open red circles are from Armbruster 1966 (mixed diet).

Feeding behavior.—Giles et al. (1986) described the feeding behavior of Northern Pike larvae as orientation, binocular fixation (on the prey), stalk, S-posture (of the tail), and strike. This sequence of events would describe the behavior of Northern Pike and Muskellunge in the present study in most instances but there were some deviations. Northern Pike and Muskellunge utilized the S-posture of the tail less often when attacking brine shrimp or small cladocerans than when attacking copepods or fish larvae. Brine shrimp and the small cladocerans were slower swimmers and may have required less effort to catch. A final step could be added to the sequence of feeding events and that is reposition. Northern Pike and Muskellunge were observed to move a short distance backwards after making a strike, returning to their original position.

Diet of wild Northern Pike and Muskellunge.—The published literature indicates that the diet of Northern Pike larvae passes through a sequence of changes where the size of zooplankters increases as Northern Pike length increases prior to feeding on fish (Hunt and Carbine 1951; Frost 1954; Franklin and Smith 1963). The laboratory experiment in the present study showed that this sequence would not be necessary for Northern Pike or Muskellunge if the appropriate fish larvae were available as a first food. The presence of prey fish larvae in the shallow marshes where Northern Pike develop might be less likely than in the more open waters where Muskellunge larvae develop. Those species that were not an appropriate size, such as Largemouth and Smallmouth Bass, were not attacked by Northern Pike. The cross-sectional area of these two prey species increased at a faster rate than did the mouth cross-sectional area of Northern Pike. All of the prey species presented to Muskellunge were attacked but Brook

Silverside proved to be an unsuitable prey even though its cross-sectional area was similar to those species that were consumed. Silverside, however, was a major component of the diets of wild Muskellunge longer than 40 mm TL (LaPan 1985) but were not important in Muskellunge longer than 80 mm TL (Farrell 1998). The cross-sectional area of Carp larvae increased at a similar rate as did bass and this may have prevented Muskellunge from continuing to consume Carp beyond a Carp TL of 15 mm. The use of mouth cross-sectional area to predict the size of potential prey may have to be modified to include the opening between the cleithra which has been shown to be less than the mouth opening in Largemouth Bass (Timmerman et al. 2000).

The diets of wild Northern Pike (up to 28 mm) contained little fish remains and may reflect the abundance of prey in specific locations rather than a selective choice. Northern Pike were piscivorous at 27 mm TL in a previous study in Flynn Bay (Hughes 1987). Northern Pike consumed Yellow Perch in the artificial feeding experiment but would be unlikely to encounter Yellow Perch during the larval period in these St. Lawrence River bays. Yellow Perch eggs are spawned in more open water areas and not in the marshes where Northern Pike would hatch. Yellow Perch were consumed by Northern Pike in Lake Windermere (Frost 1954) after Northern Pike had reached 30 mm. Fish larvae would become more important to Northern Pike in the St. Lawrence River bays as Northern Pike emigrated from the spawning marshes to the more open nursery areas. The diet of Northern Pike at lengths < 30 mm was primarily cladocerans and copepods (Frost 1954), similar to the diets in the present study and that found by LaPan (1985), Wright and Giles (1987), and

Morrow et al. (1997). Fago (1977) observed that 4.3% of wild Northern Pike (mean TL=22.9 mm) consumed fish larvae but that it was less than 10% of the diet until Northern Pike were 40 mm TL. Bry et al. (1995) found that midges were the most important food taxon in Northern Pike larger than 27 mm TL in ponds that contained only zooplankton. Golden Shiner would be a more likely prey fish for Northern Pike larvae but were not consumed by the wild Northern Pike larvae examined. The diet of wild Northern Pike was primarily copepods, cladocerans, and chironomids which would be consistent with Northern Pike remaining in the marsh areas at the lengths examined. Muskellunge diets contained Golden Shiner and Carp larvae, and fewer zooplankters. Muskellunge eggs were associated with the shallow vegetated areas in the nursery areas, generally away from the marshes where Northern Pike were spawned.

Summary.— Development of Northern Pike and Muskellunge eggs and larvae were similar in their characteristics except for denser hypaxial pigmentation in Muskellunge. Both species have adhesive eggs and adhesive papillae and exhibit attachment behavior. Northern Pike developed faster, and showed faster increases in length and weight, than did Muskellunge at all temperatures used and in both diet types. Both species can utilize fish larvae as a first food but Northern Pike are more likely to encounter zooplankton in the spawning marshes. Wild Northern Pike and Muskellunge larvae consumed primarily zooplankton but <20 mm Muskellunge consumed fish larvae.

Acknowledgments.—This research was partially funded by grants from the New York State Department of Environmental Conservation (Federal Aid in Sport Fish Restoration grant FA-5-R) and by the Wilford A. Dence Memorial Fellowship. I would like to thank John M. Farrell, Molly Connerton, Brian Smith, Greg Hoag, Rodger Klindt, Steven R. LaPan, Eric Fickbohm, and Ryan Palmer for help in various aspects of the research. Richard T. Colesante (NYSDEC Oneida Lake Fish Hatchery) provided expertise with many aspects of fish culture.

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Northern Pike and Muskellunge development, growth, and food

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APPENDIX TABLE 1.—Selected measurements of Northern Pike raised from 1994–1998. Values are means (mm \pm SD) with the range in parentheses. N is the number of observations

N	Total length	Standard length	Pre-anal length	Head length	Eye diameter	Snout length	Head width	Body width
38	8.5 \pm 0.7 (7.3–9.8)	8.4 \pm 0.7 (7.2–9.7)	6.3 \pm 0.3 (5.5–6.9)	1.6 \pm 0.1 (1.5–1.8)	0.6 \pm 0.1 (0.5–0.7)	0.2 \pm 0.1 (0.2–0.2)	1.2 \pm 0.1 (0.9–1.5)	0.5 \pm 0.1 (0.4–0.6)
36	10.9 \pm 0.6 (10.2–12.0)	10.7 \pm 0.6 (10.0–11.7)	7.6 \pm 0.4 (7.1–8.3)	1.9 \pm 0.2 (1.7–2.5)	0.8 \pm 0.1 (0.7–0.8)	0.2 \pm 0.1 (0.2–0.5)	1.5 \pm 0.1 (1.3–1.7)	0.7 \pm 0.1 (0.5–0.7)
62	13.1 \pm 0.5 (12.2–14.0)	12.9 \pm 0.5 (12.0–13.7)	8.9 \pm 0.3 (8.2–9.7)	2.8 \pm 0.3 (2.4–3.6)	0.9 \pm 0.1 (0.8–1.2)	0.5 \pm 0.2 (0.2–0.9)	1.9 \pm 0.1 (1.5–2.1)	0.8 \pm 1.5 (0.7–1.2)
32	14.9 \pm 0.6 (14.2–16.0)	14.7 \pm 0.6 (13.9–15.7)	10.3 \pm 0.5 (9.3–11.2)	3.7 \pm 0.3 (3.3–4.3)	1.1 \pm 0.1 (0.9–1.2)	0.9 \pm 0.2 (0.7–1.2)	2.1 \pm 0.1 (1.7–2.3)	1.1 \pm 0.2 (0.8–1.5)
24	16.8 \pm 0.5 (16.2–17.7)	16.5 \pm 0.6 (15.4–17.5)	11.6 \pm 0.5 (10.8–12.5)	4.5 \pm 0.4 (3.9–5.3)	1.3 \pm 0.1 (1.1–1.4)	1.3 \pm 0.1 (1.0–1.5)	2.2 \pm 0.1 (2.0–2.5)	1.3 \pm 0.1 (1.1–1.8)
27	19.0 \pm 0.6 (18.2–20.0)	18.7 \pm 0.7 (16.8–19.7)	12.9 \pm 0.4 (11.8–13.7)	5.1 \pm 0.3 (4.3–5.7)	1.4 \pm 0.1 (1.1–1.6)	1.4 \pm 0.1 (1.1–1.7)	2.5 \pm 0.1 (2.2–2.7)	1.3 \pm 0.2 (1.1–1.8)
23	20.9 \pm 0.7 (20.2–22.0)	20.6 \pm 0.6 (19.8–21.7)	14.4 \pm 0.6 (13.3–15.3)	5.9 \pm 0.4 (5.2–6.7)	1.6 \pm 0.1 (1.4–2.0)	1.8 \pm 0.2 (1.5–2.3)	2.7 \pm 0.2 (2.5–3.3)	1.6 \pm 0.2 (1.3–2.3)
20	25.2 \pm 1.7 (22.2–27.0)	23.6 \pm 1.0 (21.8–25.0)	17.2 \pm 1.1 (15.2–18.3)	7.5 \pm 0.5 (6.7–8.2)	1.7 \pm 0.1 (1.7–2.2)	2.6 \pm 0.3 (1.9–3.0)	3.1 \pm 0.2 (2.8–3.5)	2.3 \pm 0.3 (1.8–3.0)
26	29.6 \pm 1.0 (27.5–32.0)	26.9 \pm 0.8 (25.0–28.5)	20.0 \pm 0.7 (18.0–22.0)	8.8 \pm 0.5 (7.8–10.0)	2.2 \pm 0.1 (2.0–2.6)	3.2 \pm 0.2 (2.7–3.6)	3.5 \pm 0.3 (3.1–4.5)	2.9 \pm 0.5 (2.3–3.8)
12	33.1 \pm 0.9 (32.4–35.6)	29.9 \pm 1.0 (29.0–32.8)	22.4 \pm 0.9 (21.0–24.7)	10.0 \pm 0.4 (9.5–11.0)	2.4 \pm 0.1 (2.2–2.7)	3.7 \pm 0.2 (3.3–4.0)	3.8 \pm 0.5 (3.4–5.0)	3.1 \pm 0.5 (2.6–4.2)
5	39.4 \pm 1.4 (37.5–41.0)	35.9 \pm 1.2 (34.3–37.5)	27.1 \pm 0.9 (25.8–28.3)	11.3 \pm 0.5 (10.8–12.1)	2.6 \pm 0.1 (2.5–2.7)	4.4 \pm 0.4 (3.9–4.9)	5.1 \pm 0.2 (4.7–5.2)	4.4 \pm 0.1 (4.3–4.6)
3	44.5 \pm 2.2 (42.2–46.7)	40.4 \pm 2.1 (38.2–42.2)	30.7 \pm 1.3 (29.4–32.0)	12.5 \pm 0.6 (11.9–13.0)	2.8 \pm 0.1 (2.7–2.8)	4.7 \pm 0.3 (4.5–5.0)	5.9 \pm 0.3 (5.6–6.2)	5.4 \pm 0.3 (5.1–5.7)
3	51.4 \pm 3.1 (47.9–53.7)	46.1 \pm 2.4 (43.3–47.7)	35.1 \pm 2.4 (32.3–37.0)	14.8 \pm 0.2 (14.6–15.0)	3.1 \pm 0.1 (2.9–3.2)	5.9 \pm 0.3 (5.7–6.3)	6.3 \pm 0.3 (6.2–6.7)	6.2 \pm 0.9 (5.7–7.2)

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APPENDIX TABLE 1.—Selected measurements of Muskellunge raised in 1994, 1996, and 1998. Values are means (mm \pm SD) with the range in parentheses. N is the number of observations.

N	Total length	Standard length	Pre-anal length	Head length	Eye diameter	Snout length	Head width	Body width
17	9.2 \pm 0.5 (8.2–10.0)	9.0 \pm 0.5 (8.0–9.9)	6.7 \pm 0.3 (5.9–7.1)	1.2 \pm 0.1 (1.1–1.6)	0.6 \pm 0.1 (0.5–0.7)	— —	1.1 \pm 0.1 (1.0–1.5)	0.7 \pm 0.1 (0.5–0.8)
13	11.2 \pm 0.5 (10.3–11.8)	11.1 \pm 0.5 (10.2–1.7)	7.8 \pm 0.4 (7.2–8.3)	1.7 \pm 0.1 (1.5–1.9)	0.7 \pm 0.1 (0.6–0.7)	0.2 \pm 0.1 (0.2–0.3)	1.4 \pm 0.1 (1.2–1.6)	0.8 \pm 0.1 (0.7–0.8)
24	13.4 \pm 0.2 (12.7–13.9)	13.2 \pm 0.2 (12.6–13.7)	9.3 \pm 0.2 (8.9–9.6)	2.4 \pm 0.1 (2.1–2.7)	0.8 \pm 0.1 (0.7–0.9)	0.4 \pm 0.1 (0.2–0.6)	1.7 \pm 0.1 (1.6–1.7)	0.9 \pm 0.1 (0.7–0.8)
18	15.1 \pm 0.6 (14.1–16.0)	14.9 \pm 0.6 (13.8–15.8)	10.6 \pm 0.5 (9.7–11.3)	3.2 \pm 0.4 (2.5–3.7)	0.9 \pm 0.1 (0.8–1.0)	0.8 \pm 0.2 (0.5–1.1)	1.8 \pm 0.1 (1.7–1.8)	0.9 \pm 0.1 (0.8–1.2)
16	17.0 \pm 0.6 (16.1–17.7)	16.8 \pm 0.5 (15.8–17.5)	12.0 \pm 0.4 (11.2–12.5)	4.0 \pm 0.3 (3.3–4.7)	1.0 \pm 0.04 (0.9–1.1)	1.2 \pm 0.1 (1.0–1.4)	1.8 \pm 0.1 (1.7–2.0)	1.2 \pm 0.1 (0.9–1.3)
20	18.9 \pm 0.5 (18.1–19.7)	18.7 \pm 0.5 (17.8–19.5)	13.3 \pm 0.4 (12.7–14.0)	4.8 \pm 0.3 (4.2–5.2)	1.1 \pm 0.1 (1.0–1.2)	1.6 \pm 0.2 (1.2–1.7)	1.9 \pm 0.1 (1.7–2.2)	1.4 \pm 0.1 (1.2–1.7)
19	21.1 \pm 0.5 (20.1–22.2)	20.6 \pm 0.5 (19.8–21.5)	14.9 \pm 0.5 (14.0–15.7)	5.6 \pm 0.5 (4.9–6.7)	1.2 \pm 0.1 (1.1–1.4)	2.0 \pm 0.3 (1.7–2.6)	2.2 \pm 0.2 (1.8–2.5)	1.6 \pm 0.2 (1.4–2.0)
65	24.2 \pm 1.3 (22.2–26.6)	22.9 \pm 1.2 (17.9–24.9)	17.5 \pm 0.9 (16.0–19.5)	7.0 \pm 0.6 (5.8–8.2)	1.4 \pm 0.1 (1.2–1.7)	2.7 \pm 0.3 (2.0–3.4)	2.5 \pm 0.1 (2.3–3.0)	1.9 \pm 0.2 (1.5–2.7)
33	28.9 \pm 1.4 (27.1–31.9)	26.7 \pm 1.3 (24.3–29.5)	20.6 \pm 1.0 (19.3–23.0)	8.7 \pm 0.5 (7.5–9.9)	1.6 \pm 0.1 (1.5–1.8)	3.6 \pm 0.3 (3.0–4.2)	2.9 \pm 0.2 (2.5–3.2)	2.3 \pm 0.3 (1.8–3.2)
16	35.9 \pm 3.5 (32.2–41.7)	33.2 \pm 3.1 (29.8–38.2)	25.3 \pm 2.2 (22.9–29.2)	10.9 \pm 1.3 (9.0–13.0)	1.9 \pm 0.1 (1.7–2.2)	4.6 \pm 0.6 (3.7–5.7)	3.7 \pm 0.5 (3.1–4.6)	3.3 \pm 0.8 (2.4–4.7)
11	43.8 \pm 1.2 (42.2–45.6)	39.9 \pm 1.4 (38.2–42.2)	30.4 \pm 0.9 (29.0–32.0)	13.5 \pm 0.8 (12.8–15.7)	2.2 \pm 0.1 (2.1–2.2)	5.9 \pm 0.2 (5.6–6.3)	4.7 \pm 0.3 (4.2–5.2)	4.4 \pm 0.4 (3.5–4.8)
13	49.9 \pm 1.9 (47.3–53.2)	45.5 \pm 1.8 (42.8–47.7)	34.6 \pm 1.4 (32.7–36.9)	15.1 \pm 0.5 (14.6–15.9)	2.4 \pm 0.1 (2.3–2.6)	6.7 \pm 0.4 (6.2–7.4)	5.1 \pm 0.3 (4.4–5.4)	4.7 \pm 0.4 (4.2–5.6)