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Some Aspects of the Early Life History of Lake Herring in Western Lake Superior

SOME ASPECTS OF THE EARLY LIFE HISTORY OF LAKE HERRING (COREGONUS ARTEDII) IN WESTERN LAKE SUPERIOR

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ABSTRACT

During May and June of 1981 and 1982, the development, distribution and density of lake herring larvae in the Duluth-Superior area of western Lake Superior were studied. Lake herring larvae were present in the area from late April to middle June but were most abundant from middle to late May. Larvae hatched along the north shore of the lake and congregated in the area of the Duluth Harbor Entry. Mean densities in this area frequently exceeded 1000/m and were 10 to 100 times higher than those in areas along the west and south shores. Density usually decreased with distance away from the shoreline, and larvae were not found more than 6 km from shore until later in June. Although larvae were several times more abundant in the 0-2 m depth stratum, especially along the west and south shores, substantial numbers occurred in the 4-6 m stratum along the north shore.

Tentatively, we conclude that the north shore area in the vicinity of the Duluth Entry is an important developmental area for lake herring larvae. We estimate that larvae remain in this area for 14-20 days after hatching, during which time they grow from about 10 to 20 mm SL and reach the late mesolarval stage of development. Preliminary estimates of instantaneous growth rates from hatching to about 16 mm SL in 1981 and 1982 were 0.0545 and 0.0543, respectively, which we believe are overestimates. Estimates of instantaneous mortality rates for the same size intervals were 0.4110 and 0.4176 in 1981 and 0.5837 and 0.5931 in 1982, which we also believe are overestimates.

We further conclude that the Duluth-Superior area of western Lake Superior offers excellent potential for developing index stations for relating larval abundance and population dynamics to subsequent year-class strength. We also present in this report the first descriptions of Lake Superior lake herring larvae.

INTRODUCTION

Lake herring (Coregonus artedii) populations in Lake Superior historically have supported an important and productive commerical fishery both as direct-yield stocks (Baldwin et al., 1979; Anderson and Smith, 1971a; Dryer et al., 1965) and as forage-base stocks for lake trout (Hile and Buettner, 1955). Although catches of lake herring reported prior to 1929 were not separated from catches of other species of the Leucichthyes subgenus (known collectively as "chubs"), compositions of subsequent catches that were separated plus information from other historical accounts suggest that most of the early fishery consisted of lake herring (Baldwin et al., 1979). The same catch statistics also clearly document the precipitous decline in lake herring populations that occurred in Lake Superior in the mid 1950's.

Decline of coregonine populations in general has been associated variously with unfavorable interactions with exotics (Spangler, 1970; Christie et al., 1972), environmental degradation (Colby et al., 1972; Edsall and Yocum, 1972), and overexploitation (Smith, 1968; Jensen, 1976; Patriarche, 1977). Selgeby (1982) presented a convincing argument that in the case of western Lake Superior lake herring populations the decline occurred as a direct result of overexploitation. However, despite a great reduction in fishing intensity for these populations from the late 1960's to the present, lake herring abundance has remained very low.

The reasons for the failure of western populations to recover are not clear. Anderson and Smith (1971b) concluded that competition for zooplankton between the larvae of lake herring and smelt (Osmerus mordax) and, to a lesser extent, lake herring and bloater (Coregonus hoyi) had a strong negative influence on lake herring abundance. More recently, Swenson and Heist (1981) suggested that smelt predation on larval herring could account for the herring's continued low abundance in the Duluth-Superior area. Selgeby et al. (1978) found that smelt predation may be important in areas of high larval herring density (e.g., Black Bay, Ontario) but that it was insignificant in the Apostle Island region where larval herring densities were low. These studies suggest the hypothesis that high mortality during the larval period may be one reason why recruitment of adult lake herring has remained low. At the very least, these studies, as well as others (Faber 1970; Lindstrom 1970; Reckahn 1970, 1978; Viljanen 1980), clearly point to the need for a greater understanding of the ecology of larval coregonines and how their growth and mortality affects adult population size.

The present study was undertaken as a first step in elucidating the dynamics of larval lake herring in the Duluth-Superior area of western Lake Superior. Our immediate objective was to investigate the spatio-temporal distributions of lake herring larvae in the area so that index stations for measuring larval density, growth rates, and mortality rates could be established. To meet this objective it was necessary to experiment with quantitative sampling techniques and to develop methods for determining the ages of field-caught larvae so that larval catch curves could be generated.

In this report, we present data on the seasonal occurrence and distribution of lake herring larvae in the Duluth-Superior area of Lake Superior. We present preliminary estimates of larval density in 5 index areas and examine the problems associated with determining growth and mortality rates. We also provide the first descriptions of larval Coregonus artedii from Lake Superior.

METHODS

REARING OF LARVAE

Larvae of lake herring and round whitefish (Prosopium cylindraceum) were reared at the Minnesota Department of Natural Resources French River Hatchery facility. Eggs of lake herring were obtained from Brule Lake stock on 8-12 November 1981 and from Lake Superior stock caught near Bayfield, Wisconsin, on 4 December 1981. Larvae from Brule Lake stock were reared because MDNR has planted larvae from this stock into Lake Superior since 1973 (Herbert Johnson, MDNR, pers. comm.). Eggs of round whitefish were obtained from Lake Superior stock caught near the hatchery on 9-12 December 1981. These larvae were reared primarily as reference specimens for separating field caught lake herring from round whitefish.

All embryos were incubated through the winter in battery jars using water from French River. Incubation temperatures varied from 0+ to 1.0 C. In mid-April about two weeks before larvae began to hatch, French River water was replaced by Lake Superior water, which was used for the duration of the study.

As larvae hatched and swam up, they were caught in baskets placed below the battery jars. Larvae were removed from these baskets as soon as possible and placed into rearing baskets made of plexiglass and nitex netting. The rearing baskets were labelled as to species and date of hatching and placed in incubation troughs that were part of the same flow-though system as the egg batteries. Brine shrimp were provided periodically using the automatic feeding system described by Anderson (1970). However, the system frequently malfunctioned and hand feeding was added 2 to 3 times per day. Zooplankton strained from Lake Superior water were added to the diet about 4 weeks after hatching had begun.

Specimens were removed from the baskets and preserved in Davidson's solution (Lam and Rolf, 1977) on the days of hatching and every day afterward for the first 21 days. Larvae were then taken at 3-7 day intervals. The stages of morphological development were determined through time and selected specimens were measured and described according to the methods outlined below for field specimens.

In 1982, we intended to rear specimens of C. hoyi, C. zenithicus, and C. kiyi. Due to budgetary restrictions, we were unable to do so.

FIELD SAMPLING

In 1981 sampling for C. artedii larvae was carried out on 7, 15, 21,. and 28 May and 4 June at the stations indicated in

Figure 1. Larvae were captured with 3 types of samplers: a Bongo sampler (Smith and Richardson 1977), a Tucker trawl (Tucker 1951), and a meter conical net (Dovel 1964). All netting materials of all the samplers were made of nitex. The two nets of the Bongo sampler were conical (not cylindrical-conical as described by Smith and Richardson), 0.5 m in diameter at the opening, and 2.5 m deep. The mesh of the nets was 0.506 mm and 0.200 mm, respectively. The net of the Tucker trawl had a rectangular opening 1 m wide by 1.3 m high and was 5 m deep. The mesh of the netting was 0.506 mm. The Tucker trawl was rigged with a messenger apparatus for opening and closing the net (Hopkins et al. 1973). The meter net was conical, 1.0 m in diameter at the opening, 5 m deep, and made of 0.706 mm mesh netting.

The samplers were towed, usually 2 at a time in various combinations, from the Research Vessel L.L. Smith, Jr. (University of Wisconsin-Superior). Each sampler was equipped with a calibrated General Oceanics Model 2031 flowmeter for measuring the volume of water strained. Depressors were used on the Bongo and meter net samplers; the Tucker trawl frame itself was weighted. Depths of the samplers were determined from the angles and lengths of the towing cables. Sampling location and speed of the tow were determined by Loran C instrumentation, and water depth was determined by sonar. Because we were attempting to determine the best way to deploy samplers from the vessel and because the vessel's speed was hard to control precisely, the towing times and speeds varied considerably during the 1981 sampling period. We began making 12 to 15-minute tows on 7 May but reduced the time to 10 minutes on later dates. Towing speeds usually tapered from 2.2 to 1.5 m/sec during the tows. Towing was initiated from the sides of the vessel, well forward of the stern, and every effort was made to keep the samplers away from the prop wash. In 1982, the sampler used in the surface stratum was towed from a bow davit that kept it free from both the bow and stern wakes.

In 1981 12 sets of paired samples were collected with the Bongo sampler and Tucker trawl, and 10 sets were collected with meter net and Bongo sampler in order to compare relative catch efficiencies. All samples were collected during daylight hours, except on 28 May when 8 samples were collected along the north shore between 2330 hrs (28 May) and 0100 hrs (29 May). These samples were collected at 3 locations sampled between 1300 and 1430 hrs on 28 May.

In 1982 sampling was conducted on 23 April; 7, 14, 24, 28, and 30 May; and 3, 11, and 18 June at the stations designated in Figure 1. Normally, two Tucker trawls were deployed during each tow, one sampling the 0-2 m stratum and the other sampling the 4-6 m stratum. For purposes of analyzing the distribution of larvae, the study area was divided into 5 zones (Figure 1) that

were sampled during each excursion. Water temperatures in these zones were measured to a maximum of 10 m depth at 1 m intervals with a YSI telethermister that was checked against a primary standard mercury thermometer. Transparency was measured with a Secchi disc.

ANALYSIS OF FIELD COLLECTIONS

Some specimens collected from Lake Superior were examined while alive to check for pigmentation characteristics that might be lost after preservation. Specimens were preserved in Davidson's solution and returned to the laboratory for analysis. In 1981, the standard and total lengths of representative specimens in good condition were measured with an ocular micrometer to the nearest 0.1 mm. Based on the standard length data, length categories for the larvae were set up, and most specimens in good condition were measured and assigned to a length category. All specimens captured during the day on 28 May were counted but large samples were divided roughly into thirds by eye and 1/3 of each sample was measured. Specimens collected in 1982 were treated in a similar way, except that 4 very large samples were subsampled using a Folsom zooplankton spliter. Specimens that could not be assigned a length category because of their poor condition were counted and apportioned to length categories according to the percentage compostion of the measured specimens in the sample. The catch per effort (CPE) for each length group in each sample was calculated by dividing the number of specimens by the volume of water strained (m^3). The quotient was multiplied by 1000 to yield a CPE equal to the number of larvae per 1000 m^3. This expression of CPE will be used throughout this report. The paired catch statistics of the different samplers used in 1981 were determined and compared using a Student's paired t-test.

Preliminary larval growth rates were estimated from the 1981 and 1982 catch data using the methods of Hackney and Webb (1978). These estimates were used to determine the age associated with various length groups. Larval catch curves were then determined and instaneous mortality rates were estimated. Growth increment and mortality rate data from the literature and information from our reared lake herring were used to help assess the suitability of using the above methods on Lake Superior lake herring.

In order to establish the identity of field specimens and to provide data for the description of field caught lake herring, representative specimens were selecced from samples collected throughout both field seasons and were examined in detail. Up to 14 morphometric measures were made on larvae with yolk sacs and up to 11 were made on mesolarvae (Figure 2). All measurements were made with calibrated ocular micrometers. Measures followed the methods of Fuiman (1979), except that body

depth was measured below the middle of the dorsal fin anlage and at the point of greastest depth over the yolk sac. Measurements of the yolk sac length and depth and oil globule diameter were taken as shown in Figure 2. In addition, preanal and postanal myomeres were counted. The preanal count began at the myomere into which the pelvic bud was inserted and ended with the last myomere to be dissected by a line perpendicular to the posterior margin of the vent. The postanal myomere count ended with the last myomere whose dorsal and ventral lobes could be distinguished. The number of actinotrichia (fin ray bases that give rise to the fin rays) and lepidotrichia (developing or developed fin rays as used here) also were counted when present in the caudal, anal, and dorsal fin anlages.

DESCRIPTION OF THE STUDY AREA

The extreme western portion of Lake Superior is a relatively shallow water habitat that is strongly influenced by the nutrient rich discharges of the St. Louis and Nemadji Rivers. It also is influenced by plumes of red clay turbidity that come from the Nemadji and other southshore streams (Swenson 1978). The distribution of the plumes is usually along the southshore but may reach all the way to the northshore under certain weather conditions, thus affecting water clarity throughout the area. The maximum water depth in this area is 46 m and the average is 31 m. The following are brief descriptions of the zones sampled in 1982 (parts of which also were sampled in 1981).

The zone designated Northshore I (NS I) extended from the Duluth entry to just east of the mouth of the Lester River. This zone included stations CC, D, and E in Figure 1. The water in this zone was influenced by the discharge of the St. Louis River and, to a lesser extent, by the upwelling and counter-clockwise currents from farther up the northshore. Strong winds from the east and southeast frequently pushed turbid surface water into the zone from the southshore. The western end of the northshore basaltic trench extended through this zone giving it an irregular bottom and a sharply increasing water depth within a few hundred meters of the shoreline. Water depths at the sampling stations ranged from 6 to 16 m.

The zone designated Northshore II (NS II) extended from the mouth of the Lester River to 2.5 km southwest of the Talmadge River and included stations AA, A, B, and C in Figure 1. The water in this zone was often much colder and clearer than that of NS I due to lesser influence from the St. Louis River and greater influence from northshore stream runoff and lake upwelling (Table 1). However, there were occassions when warm and turbid water from the southshore extended into this zone. The shoreline relief in this zone was a bit steeper than in NS I, and depths at the sampling stations ranged from 6 to 32 m.

The westshore zone (WS) extended from the south side of the Duluth Entry along Minnesota Point to the Superior Entry and included stations F and G in Figure 1. Water in this zone usually was a little warmer than either of the northshore zones (Table 1). Cold water upwelling was not a factor here, and the sandy bottom and more gradual slope allowed faster warming in the spring. The water often was turbid as a result of local wave action and the movement of southshore water into the area under certain weather conditions. Depths at the samping stations ranged from 6 to 8 m.

The Southshore I zone (SS I) extended from the west end of the southshore to the mouth of the Amicron River and included stations W, WW, X, XX, and YY of Figure 1. The Southshore II zone (SS II) extended from the mouth of the Amicron River to the mouth of the Popular River and included stations Y, Z, and ZZ. Both SS I and SS II were stongly influenced by the turbid discharges of the Nemadji River and other southshore streams. As a result, they usually were the most turbid zones. They also were the warmest zones due to the influence of stream runoff and faster spring warming of the shallow water (Table 1). The bottom was sand with red clay sediment, and the slope was very gradual. Depths at the sampling stations ranged from 6 to 8 m.

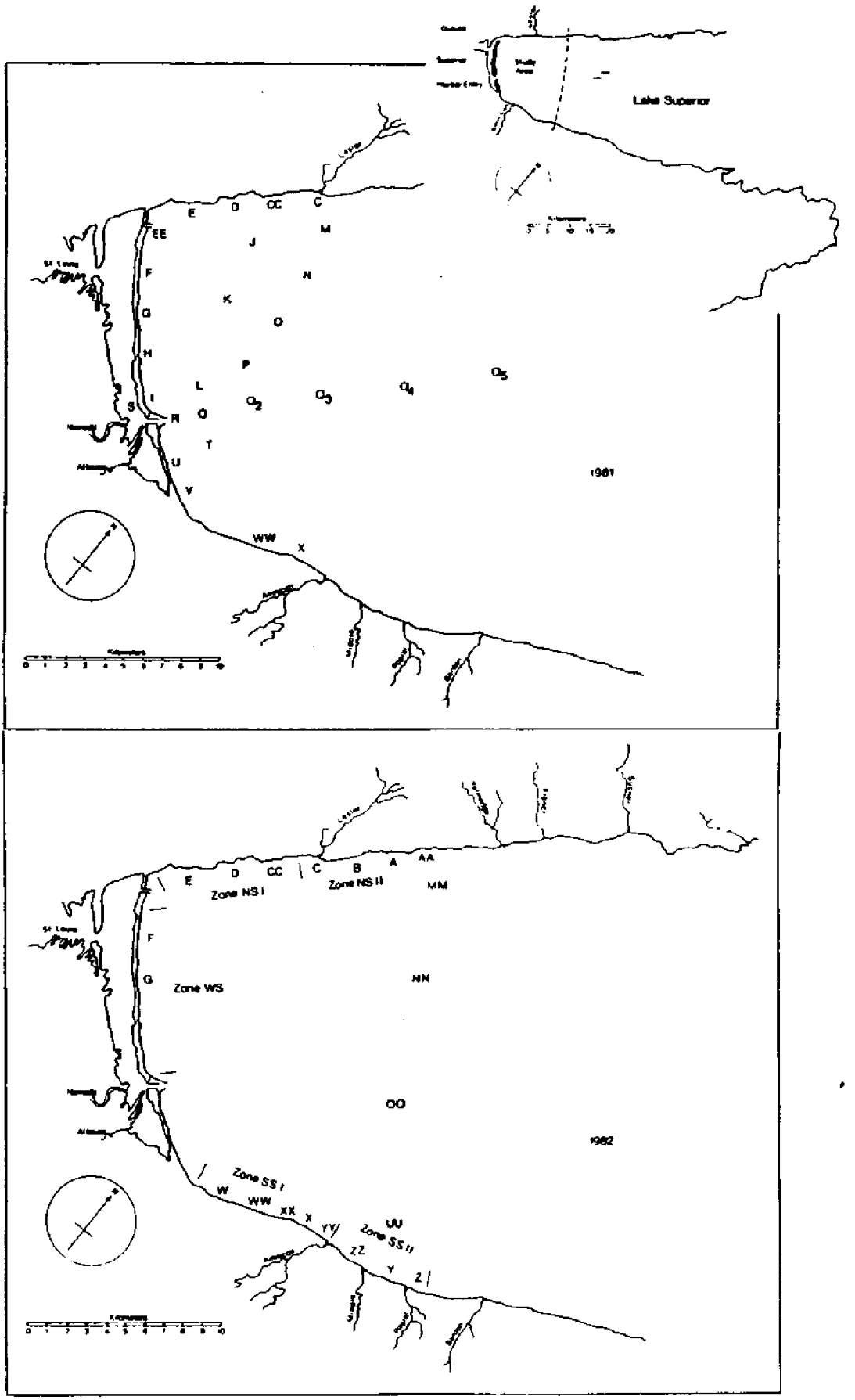

Figure 1. Duluth-Superior area of western Lake Superior showing stations and zones sampled for lake herring larvae in 1981 and 1982.

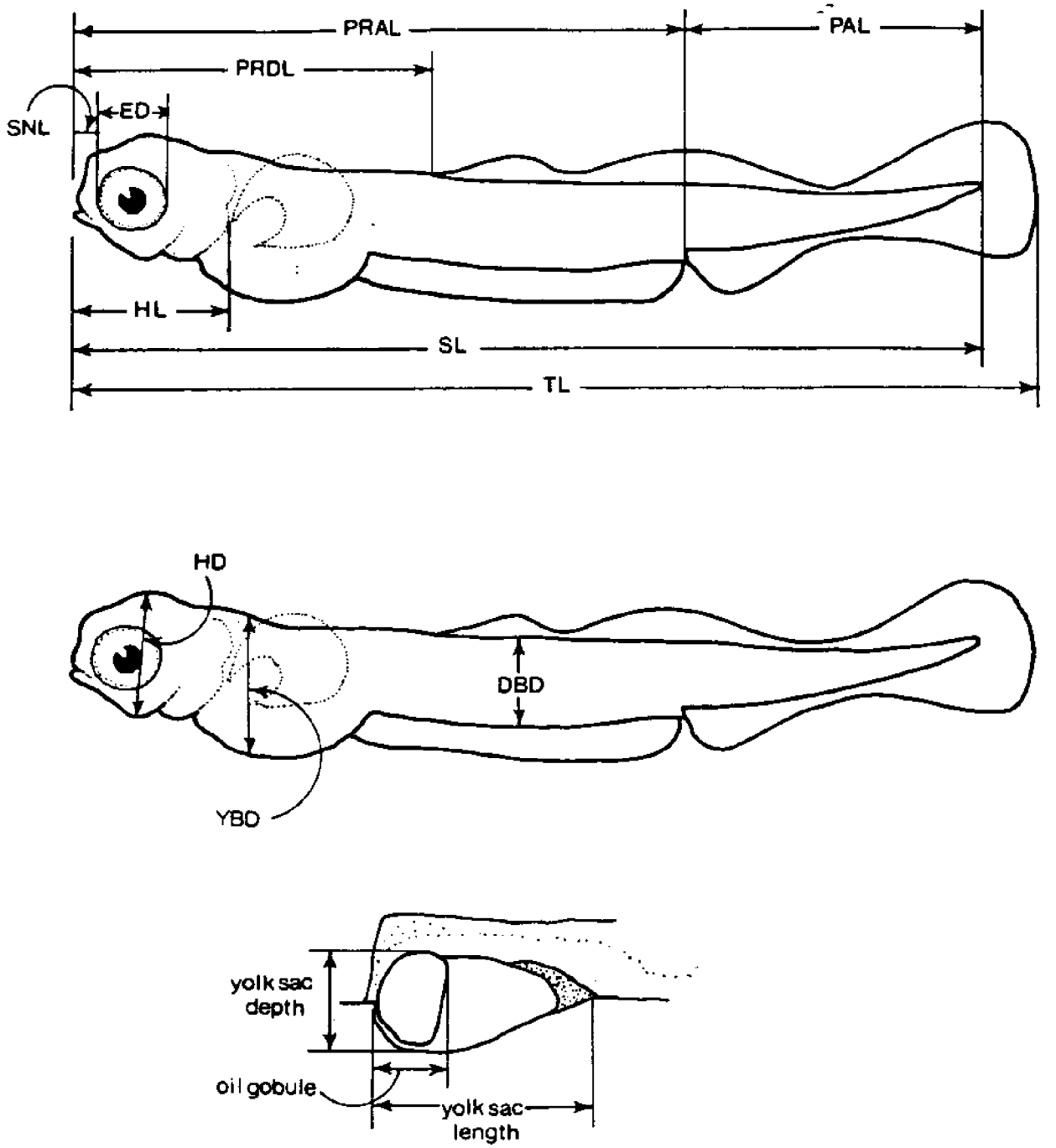

Figure 2. Morphometric measures made on larval lake herring. DBD=body depth under dorsal fin; ED= eye diameter; HD= head depth; HL= head length; PAL= postanal length; PRAL= preanal length; PRDL= predorsal length; SL= standard length; SNL= snout length; TL= total length; YBD= greatest body depth over the yolk sac.

Table 1. Summary of Lake Superior water temperatures measured during the 1982 sampling period. S = 0-2 m stratum, D = 4-6 m stratum. Temperatures are mean temperatures of the stratum given to the nearest 0.5 C.

Dates/ Strata		ZONES NS II	NS I*	W S	SS I	SS II	Deep
May 7	S	3.0	3.0/	4.0	7.5	7.0	- -
	D	2.5	3.0/	3.5	7.0	6.5	- -
May 14	S	- -	3.0/	8.5	7.0	- -	- -
	D	- -	2.5/	8.0	6.0	- -	- -
May 24	S	3.5	/13.0	12.5	10.5	8.5	- -
	D	3.0	/ 4.5	8.0	10.0	7.0	- -
May 28	S	- -	14.0/	13.0	- -	8.5	- -
	D	- -	6.5/	11.5	- -	5.5	- -
May 30	S	10.5	- -	13.0	16.5	16.5	- -
	D	4.0	- -	8.0	12.5	11.0	- -
Jun 3	S	5.0	7.5/10.5	11.0	10.5	11.0	- -
	D	4.5	6.5/ 9.0	9.5	9.5	10.0	- -
Jun 11	S	5.5	6.0/ 7.0	9.8	10.0	10.0	- -
	D	4.5	5.5/ 7.0	9.0	10.0	10.0	- -
Jun 18	S	- -	/12.5	- -	12.0	10.0	11.0
	D	- -	/12.0	- -	11.0	9.5	10.5

* Numbers to left of slash from station CC and numbers to right from station E.

RESULTS AND DISCUSSION

IDENTIFICATION OF FIELD SPECIMENS

We have identified our field specimens as Coregonus artedii Lesueur based on several considerations. There is little question that larval C. clupeaformis and Prosopium spp. can be separated from the larvae of the subgenus Leucichthys, to which C. artedii belongs, based on the studies and discriptions of Hart (1930), Pritchard (1930), Fish (1932), Price (1935), Normandeau (1963), Faber (1970), and Hinrichs (1979). The marjority of our field specimens clearly are Leucichthys, and they are morphologically and developmentally indistinguishable from the Lake Superior and Brule Lake C. artedii that we reared. Most of our field specimens do not have dorsal melanophores larger than the width of a myomere, which is a characteristic ascribed by Hinrichs (1979) to C. hoyi. (However, about 5% of both our field specimens and our hatchery reared C. artedii displayed this characteristic).

Perhaps a more important consideration is that of seasonal habitat. In the Bay of Quinte, Lake Ontario, where C. artedii was the only Leucichthys species present, Pritchard (1930) found larvae in May in shallow water near the surface. Likewise Clady (1976) reported that C. artedii larvae in Oneida Lake were concentrated in the upper 2 m of water near shore during May. In contrast, Wells (1966) reported that larval C. hoyi in Lake Michigan were concentrated near the bottom in waters 90-110 m deep. In May, Wells found very few larvae in water less than 45 m deep and he found none in water less than 18 m deep. These studies and others indicate that larval Leucichthys captured in May and early June near the surface in nearshore waters should be C. artedii. This habitat criterion along with knowledge of spawning grounds has been used previously by Faber (1970) and Selgeby et al. (1978) to identify captured larval Leucichthys as C. artedii.

At present, we do not know what the larvae of C. kiyi and C. zenithicus look like, nor do we have any information on their seasonal occurrence and distribution. However, based on what is known about the adult distribution and spawning (Scott and Crossman 1973), we would expect to find few of their larvae in shallow surface waters in May and early June. Thus, despite the absence of descriptions and reference specimens of the latter two species, we believe we are justified in identifying our specimens as C. artedii. Further, we have been conservative in our identifications and have not included specimens with large dorsal melanophores in our quantitative analyses, despite their resemblance to reared C. artedii. Several specimens collected in April and May 1982 also were excluded because of their large size yet early stage of development.

DESCRIPTIONS OF LAKE SUPERIOR LAKE HERRING LARVAE

Because of their recent speciation, subsequent hybridization and introgression, and high degree of phenotypic plasticity, coregonine fishes have presented a considerable taxonomic problem (Svardson 1979; Todd et al. 1981). The fact that adult populations exhibit a high degree of environmentally induced variation implies that larval populations do as well. Because lake herring larvae from Lake Superior (reared or wild caught) have never been described, we provide below detailed descriptions of our field specimens pointing out the morphological variation that we observed. We use the basic terminology of Snyder (1976) for phases of development during the larval period. We further subdivide the phases into several standardized stages that we believe may help us in future to provide relative age brackets for field specimens. At a later time, we hope to provide line drawings to accompany the descriptions.

Protolarval Phase

Early Protolarvae--ranged in size from 8.8 to 12.2 mm SL (9.2 to 12.8 mm TL) but usually were 10.0 to 11.5 mm SL. This stage was characterized by the presence of large, bright yellow yolk sacs (usually greater than 1.5 mm long and 0.7 mm deep); small, blunt snouts; subterminal mouths with the lower jaw extending only to the anterior margin of the eye; the absence of actinotrichia in all fin fold anlages; and the absence of dorsal flexure of the notochord in the caudal fin fold. Exogenous feeding began during this stage (37 of 80 specimens 10.7-11.5 mm SL had food in their gastrointestinal tracts). A summary of morphometry and myomere counts for this stage is given in Tables 2 and 3.

Late Protolarvae--ranged in size in from 11.5 to 14.3 mm SL (12.0 to 15.2 mm TL) but usually were 12.0 to 13.0 mm SL. This stage was characterized by a noticeably reduced amount of yolk (yolk sac usually less than 1.4 mm long and 0.6 mm deep), a more obvious snout, a lower jaw usually extending somewhat beyond the eye, and the presence of at least 2 actinotrichia but no lepidotrichia along the ventral aspect of the notochord in the caudal fin fold. Actinotrichia did not form in the dorsal and anal fin anlages during this stage. A slight dorsal flexure of the notochord was evident in a small number of specimens, but usually flexure occurred in the early mesolarval stage. The oil globule and some yolk material were still present at the end of this stage, although the amount varied greatly, especially in larvae from later hatching cohorts. We noted that many of the 11.5-12.5 mm SL specimens collected 24 May 1982 had less yolk than did some of the 13-14 mm SL specimens collected 14 May 1982. Thus, yolk may be used up relatively faster by protolarvae from later hatching cohorts. Morphometry and

myomere counts for this stage appear in Tables 2 and 3.

Protolarval Pigmentation--The yolk material in living specimens was bright yellow with small flecks of light orange. The oil globule was translucent and a rather deep orange color. No other xanthophyllic pigmentation was noted.

The number, size, shape, and distribution of melanophores was extremely variable. This was true for hatchery reared specimens as well as wild caught. In general, protolarvae were not nearly so heavily pigmented as those described by Pritchard (1930) and Fish (1932). Nor were the melanophores as regularly arranged as those depicted by Faber (1970). The amount and pattern of pigmentation more closely resembled the descriptions of Hinrichs (1979), except that both hatchery reared and wild caught larvae frequently possessed dorsal melanophores that were larger than the widths of the myomeres.

Early protolarvae had 3-22 melanophores on the dorsal surface of the postorbital region of the head. Some of these were contracted and others were ovate stellate. Usually, one to several contracted melanophores were present on the nape. Normally, fewer than 10 melanophores were present on the predorsal area. They were widley spaced and arranged irregularly with respect to right and left myomeres. Dorsal melanophores became more numerous caudally, such that the dorsal aspect of the caudal peduncle had 1 or more contracted melanophores per myomere. Small melanophores were present along the dorsal and ventral aspects of the caudal notochord. Generally, dorsal melanophores were smaller than the width of a myomere. However, about 5% of the wild caught and reared specimens exhibited more than 2 ovate stellate dorsal melanophores that were larger than the width of a myomere. About 20% of the early protolavae examined from the field were immaculate on the head, nape, and predorsum, and they possessed fewer melanophores in all other areas. About 10% of the reared specimens showed this very sparse pigmentation.

The occurrence of melanophores on the yolk sac also was highly variable. Sometimes there were only a few small, concentrated melanopores over the oil globule and a few more on the lateral aspects of the yolk sac. In the other extreme, many small, stellate melanophores were scattered over the entire lateral and ventral surfaces of the oil globule and yolk sac. The shapes of individual melanophores varied from round and square stellate to streaked.

All specimens showed a series of well-developed and fairly regularly spaced melanophores along the dorsolateral aspects of the intestine, beginning on the caudal one-third of the yolk sac and extending to the vent. Again, the size and shape of melanophores varied greatly, but their regular arrangement was

always conspicuous in lateral view. Some specimens possessed a few scattered superficial melanophores more laterally on the intestine. The number of these tended to increase throughout the phase. Pigmentation on the ventral aspect of the caudal peduncle resembled that of the dorsal aspect, except that fewer melanphores were present. The myomeres of protolarvae were not pigmented laterally.

Mesolarval Phase

Early Mesolarvae--ranged in size from 12.6 to 17.2 mm SL (13.1 to 18.5 mm TL) but usually were 13.0 to 14.5 mm SL. This stage was characterized by the presence of at least 2 distinguishable caudal lepidotrichia in the caudal fin fold, the presence of well defined maxillary bones, and the absence of pelvic fin buds. Caudal lepidotrichia first formed in the ventral protion of the fin anlage, where 3-5 rudimentary rays were evident in most speicmens longer than 13.0 mm SL. Usually very little dorsal flexure of the urostyle had occurred by this time, but by the end of this stage a 10 to 20 degree flexure had occurred. Actinotrichia formed in the anal and dorsal fin anlages during this stage. They formed at about the same time, although they were often better developed in the anal anlage suggesting a slightly earlier development there. The latter observation differs from that of Pritchard (1930) and of Hinrichs (1979). Anal and dorsal actinotrichia generally formed after urostyle flexure. Anal and dorsal lepidotrichia did not develop during this stage.

Nearly all early mesolarvae lost all traces of yolk and oil globule materials by the time they reached 14.0 mm SL. The largest larvae with visible oil globule material was 15.1 mm SL. In June 1982, few mesolarvae longer than 13.5 mm SL possessed yolk or oil globule remants, again suggesting a slightly faster absorption rate relative to size for later hatching cohorts. The disappearance of yolk material tended to precede slightly the first evidence of anal fin actinotrichia.

At about 13.5 mm SL the outline of the maxillary bones became visible. These bones were well formed and conspicuous in mesolarvae prior to the formation of pelvic buds. The lower jaw at this time extended anteriorly and dorsally of the eye to the level of the pupil making the mouth nearly terminal. Morphometry and myomere counts for this stage appear in Tables 2 and 3.

Mesolarvae II--ranged in size from 14.0 to 21.0 mm SL (14.6 to 22.1 mm TL) but usually were 16.0 to 19.0 mm SL. This stage was characterized by the presence of pelvic fin buds and the absence of well defined anal and dorsal fin lepidotrichia. During this stage the anal and dorsal fin actinotrichia reached full development, and the anal and dorsal fin anlages became

more clearly demarcated as the fin fold degenerated. Dorsal flexure of the urostyle surpassed 45 degrees by the end of this stage, and segmentation could be seen in some of the caudal lepidotrichia. No ray development of any kind was evident in the pectoral or pelvic fins.

Mesolarvae III--ranged in size from 19.1 to 22.4 mm SL (22.1 to 24.1 mm TL). Few larvae of this stage were collected, but most were over 21 mm SL. The stage was characterized by the presence of anal or dorsal fin lepidotrichia, usually both. The dorsal fin fold of all mesolarvae III specimens was discontinuous between the dorsal and adipose fins (some mesolarvae II showed this characteristic), and the anal fin was clearly demarcated. The largest, most completely developed specimen collected still did not have a full complement of median fin rays, nor did it show evidence of forking in the caudal fin. There was still no evidence of ray formation in the pectoral or pelvic fins in this specimen, although the pelvic fins were over 1 mm long. Modes of morphometry and myomere counts are not reported in Tables 2 and 3 for this stage due to the small sample size.

Mesolarval Pigmentation--The number of melanophores increased gradually during the mesolarval phase. In the early mesolarval stage, most of the parietal area of the head was covered by a combination of stellate and small contracted melanophores. Small contracted melanophores were also present in the occipital region and on the snout. Most early mesolarvae had formed two more or less uninterrupted rows of melanophores extending from the predorsus to the tip of the urostyle. Often these dorsal rows became more regular and were more dense from the dorsal fin anlage to the middle of the caudal peduncle. Along this area many specimens displayed regular pairing of melanophores on either side of the fin fold, a pattern associated with C. clupeaformis larvae. Often the ovate stellate melanophores in this region were larger than the myomere widths (in both reared and wild caught specimens). Ventrally, the anterior margin of the yolk sac remnant became demarcated from the isthmus by a line of melanophores that extended laterally to the ventral insertions of the pectoral fins buds.

By the end of the early mesolarval stage, more melanophores were present laterally along the intestine and on the ventral caudal penduncle. Several small but conspicuous melanophores were present on each opercle. The pigmentation patterns of mesolarve II and III were similar to that of early mesolarvae except that the pigmentation was more intense. More melanophores were gradually added along the dorsus and some extended onto the dorsolateral aspect of the body. Additional melanphores developed laterally and superficially to the intestine. No pigment developed in dorsal, anal, or lateral fins.

Table 2. Summary of morphometry of larval lake herring collected from western Lake Superior, 1981-82. (TL=total length; SL=standard length; PRAL=preanal length; PDL=predorsal length; HL=head length; HD=head depth; DBD=body depth under dorsal fin; YBD=greatest body depth at the yolk sac; ED=eye diameter; YSL=yolk sac length; YSD=yolk sac depth; OGD=oil globule diameter).

Charac-	PROTOLARVAE				MESOLARVAE				
	early		late		early		II		III
ter	range	mode	range	mode	range	mode	range	mode	range mode*
TL	9.2		12.0		13.1		14.6		22.1
	-12.8		-15.2		-18.5		-22.1		-24.1
SL	8.8		11.5		12.6		14.0		19.1
	-12.2		-14.3		-17.2		-21.0		-22.4
PRAL/	0.63	0.65	0.64	0.66	0.62	0.66	0.64	0.67	0.66
TL	-0.68		-0.68		-0.68		-0.71		-0.68
PDL/	0.29	0.33	0.30	0.35	0.38	0.42	0.39	0.43	0.41
TL	-0.40		-0.38		-0.43		-0.46		-0.45
HL/	0.14	0.15	0.14	0.16	0.15	0.17	0.15	0.17	0.15
TL	-0.17		-0.18		-0.17		-0.18		-0.18
HD/	0.10	0.11	0.09	0.12	0.10	0.11	0.10	0.10	0.10
TL	-0.13		-0.12		-0.11		-0.12		-0.11
DBD/	0.06	0.07	0.07	0.07	0.08	0.08	0.07	0.09	0.09
TL	-0.08		-0.08		-0.10		-0.10		-0.10
YBD/	0.11	0.12	0.09	0.10	0.07	0.08			
TL	-0.12		-0.11		-0.10				
ED/	0.35	0.39	0.33	0.41	0.36	0.36	0.34	0.36	0.31
HL	-0.44		-0.47		-0.38		-0.38		-0.38
YSL	1.5		0.9						
(mm)	-2.1		-1.5						
YSD	0.7		0.5						
(mm)	-0.8		-0.7						
OGD	0.5		0.2						
(mm)	-0.7		-0.5						
N	10		10		10		10		4

*Mode not reported due to small N

Table 3. Summary of myomere counts of larval lake herring collected from western Lake Superior, 1981-82. (PAM=preanal myomeres; PtAM=postanal myomeres; TotM=total myomere count).

	PROTOLARVAE				MESOLARVAE					
	early		late		early		II		III	
Count	range	mode	range	mode	range	mode	range	mode	range	mode*
PAM	38 -41	39	39 -41	40	38 -42	40	38 -42	40	38 -41	
PtAM	15 -18	17	16 -18	17	16 -17	16	15 -18	16	15 -16	
TotM	55 -58	56	56 -57	57	54 -58	56	54 -58	56	53 -56	
N	10		10		10		10		4	

*Mode not reported due to small N

COMPARISONS OF THE SAMPLERS

The catches and corresponding CPE's from the paired sampling tests are given in Table 4. Surprisingly, the side of the Bongo sampler with the 0.200 mm mesh size always caught nearly the same number of larvae as the side with the 0.506 mm mesh size. Paired t-tests showed no significant differences for number of larvae caught or CPE at $P>0.05$. The meter net often caught as many total larvae as the Bongo sampler, but its CPE's were fairly consistently and significantly (0.05 level) lower than those of the Bongo sampler. This was expected because the bridles preceding the meter net would tend to increase larval avoidance.

The Tucker trawl caught more total larvae than did the Bongo sampler during every test. However, because it filtered nearly four times as much water during each run, its CPE's were sometimes lower than those of the Bongo sampler. The differences between Tucker trawl and Bongo sampler CPE's were not significant. Based on these results we estimated larval densities only from Bongo sampler and Tucker trawl catches in 1981.

Although the Bongo sampler and Tucker trawl yielded similar estimates of density (CPE), we decided to use Tucker trawls in 1982 for two reasons. For the same amount of towing time, Tucker trawls provide more total larvae, especially in areas of low density (Table 4). Relatively large numbers of larvae are desirable when length frequencies need to be reliably determined. Also, since Tucker trawls can be opened and closed, they can sample descrete depth strata without contamination from other strata.

SEASONAL OCCURRENCE, RELATIVE ABUNDANCE, AND DISTRIBUTION

Seasonal Occurrence and Relative Abundance

During 1981 and 1982 respectively, a total of 8013 and 8354 lake herring larvae were collected from western Lake Superior. Table 5 summarizes the catches for each sampling excursion during the two years. Larval lake herring were present in the study area on every sampling date, but their relative abundance as measured by CPE was highly variable through space (as will be shown later) and time (Fig. 3). In 1981, mean CPE remained near or above 200 throughout May, but fell to 18 by 4 June. In contrast in 1982, mean CPE remained well below 100 until 24 May. It reached a peak around 28 May and remained above 100 into June. By 11 June mean CPE had fallen sharply to 4. Plots of maximum CPE showed the same seasonal patterns of relative abundance as did mean CPE (Fig. 3).

We were unable to determine a precise period when hatching

Table 4. Paired sample catches used to evaluate relative catch efficiencies of the three samplers used in 1981. Catches with CPE's less than 1 were not used in paired t-test analyses.

Meter Net		Bongo 200		Bongo 506		Tucker trawl	
Catch	CPE	Catch	CPE	Catch	CPE	Catch	CPE
81	78.2	48	158.2	37	122.0		
94	118.4	21	109.1	14	72.8		
418	610.5	451	2520.7	316	1766.2		
65	84.8	46	254.9	47	260.5		
34	49.8	110	611.1	144	800.0		
4	6.0	0	0.0	0	0.0		
2	0.8	0	0.0	0	0.0		
		16	84.9	16	84.9	125	98.5
		45	214.1	51	244.7	122	87.3
		12	57.9	6	28.9	46	32.9
		9	47.1	6	31.4	37	50.5
		105	542.7	96	496.2	427	340.2
		27	136.0	48	241.7	149	111.8
				24	125.4	64	48.5
				2	10.8	8	11.9
				3	17.7	42	55.8
				2	10.0	23	23.8
				4	21.7	10	9.6

Table 5. Summary of catches of larval lake herring from western Lake Superior, 1981-82. Catch per effort (CPE) is the total number of larvae caught per 1000 m of water filtered. Mean CPE is the sum of the sample CPE's divided by the number of samples containing larvae.

		Sampling Dates							
1981		5/7	5/15	5/21	5/28	5/28	6/4		
Mean CPE		311	446	3	181	255	18		
Range		78	4	2	14	49	3		
CPE		-942	-2521	-9	-1384	-543	-56		
No. Larvae		686	2149	5	4111	940	122		
No. Measured		602	1898	3	1239	870	103		
No. Samples with larvae		8	20	4	20	8	14		
Total Samples		15	29	18	26	8	17		
1982	4/23	5/7	5/14	5/24	5/28	5/30	6/3	6/11	6/18
Mean CPE	<1	9	31	96	299	169	136	4	2
Range	<1	1	1	1	4	1	2	1	1
CPE		-27	-109	-980	-1118	-1003	-1079	-14	-6
No. Larvae	3	182	385	1887	1554	1796	2486	31	33
No. Measured	3	174	360	1091	324	770	1040	31	30
No.Samples with larvae	2	13	11	19	4	10	17	8	8
Total Samples	3	20	14	24	10	14	24	24	20

1 Samples not from normal study are, not included in late analyses.
2. Day samples (1300-1430 hrs)
3. Night samples (2330-0100 hrs)

of lake herring began in each year. However, it is clear from the presence of 17 mm and longer metalarvae in the 7 May catches of 1981 and 1982 (Figs. 4 and 5) that at least one cohort of lake herring had hatched well before the first of May in both years. The fact that only 1 newly hatched larva (10-11 mm) was collected on 23 April 1982 suggests that the first major hatch occurred during the last week of April in 1982. In 1981, the predominance of 12 mm larvae on 7 May shows that another cohort hatching series was well under way by that time. This cohort was discernable throughout the sampling series, and there was little evidence of substantial recruitment of other hatching cohorts (Fig. 4). In contrast, the 1982 length frequency data show that a new cohort had just begun hatching on 7 May and that substantial hatching continued well into May (Fig 5).

Larval lake herring were still present in the study area on the last sampling date of each year (4 June 1981 and 18 June 1982), but their abundance was very low. The movement out of the study area in June was not size specific, suggesting that some physical or biotic factor unrelated to ontogeny caused the emigration. Regardless of size, lake herring larvae usually are not found in this area after mid-June (M. Balcer and W. Swenson, Center for Lake Superior Environmental Studies, University of Wisconsin-Superior, pers. comm.).

The seasonal abundance pattern described above is similar to the one found by Anderson and Smith (1971) for coregonine larvae collected in the Duluth-Superior area in 1967 and 1968. Selgeby et al. (1978) also reported a similar seasonal pattern for lake herring larvae collected in the Apostle Islands region and to a lesser extent in Black Bay in 1974. Although we must keep in mind the number of years between Selgeby's study and ours, it is encouraging to note that our peak relative abundance estimates are similiar to those from Black Bay. According to Selgeby et al., Black Bay accounted for over 50% of the total Canadian catch of lake herring from Lake Superior during 1960-1974. Larval relative abundance in Black Bay was more than 100 times that of the Apostle Islands in 1974.

Distribution

In 1981 samples were taken in a variety of locations to give us a preliminary idea of the where lake herring were located. We concentrated the sampling in the upper 2 m of water column based on the results of Anderson and Smith (1971) and Selgeby et al. (1978). Generally, larvae were more abundant nearshore than offshore, and they were particularly abundant in the area around the Duluth entry (Fig. 6). Lake herring larvae were not found in deep, open waters sampled on 7 and 21 May.

The 1982 sampling was more systematic and included 4-6 m depth samples as well as upper 2 m samples. These results suggest several trends. First, CPE was consistently highest

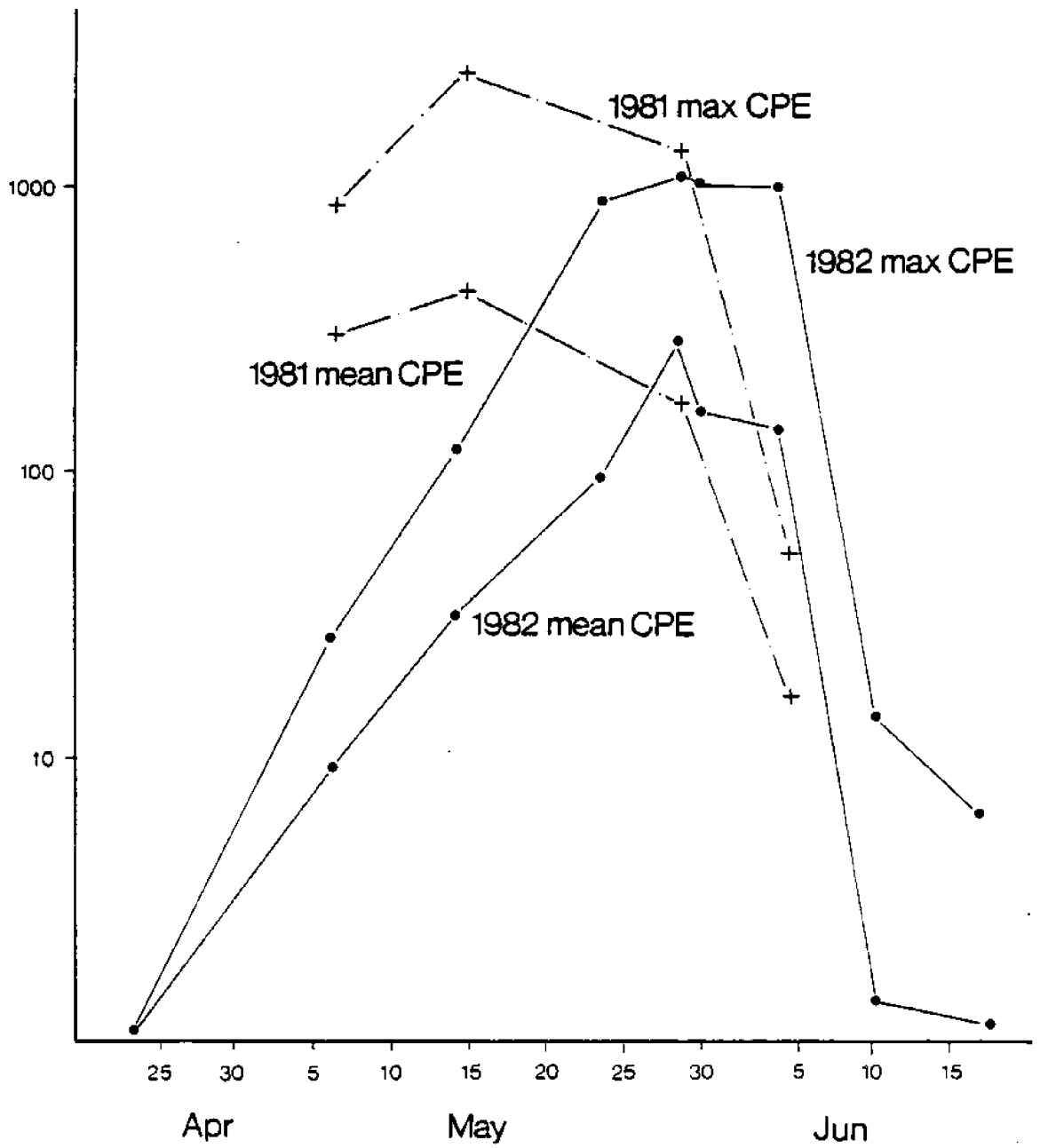

Figure 3. Mean and maximum CPE (no./1000 m) of lake herring larvae collected in western Lake Superior in May and June of 1981 and 1982.

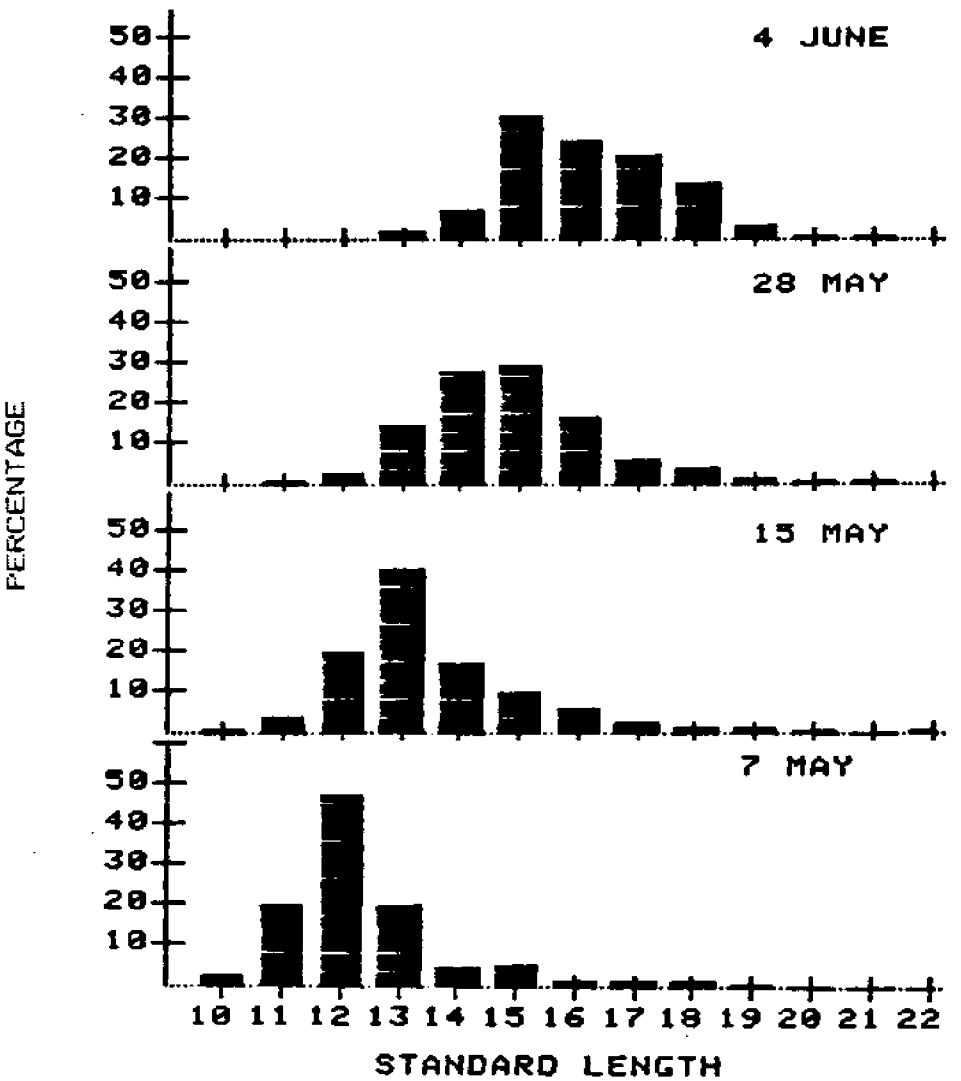

Figure 4. Length frequency distribution of lake herring larvae collected in western Lake Superior 7 May - 4 June, 1981.

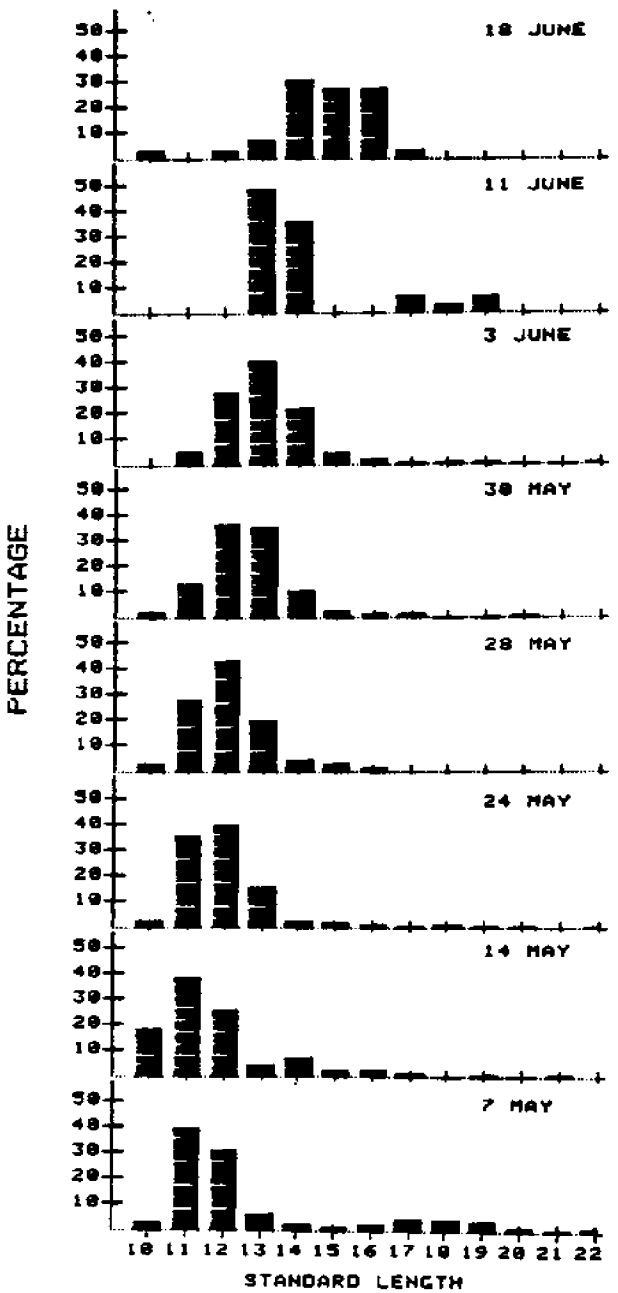

Figure 5. Length frequency distribution of lake herring larvae collected in western Lake Superior 7 May - 18 June, 1982.

along the north shore, especially in zone NS I, which is in the area of the Duluth Harbor Entry (Figs. 7 through 13). The length frequency patterns (based on CPE) strongly suggest that larvae were hatching somewhere along the north shore and were congregating (or hatching) in NS I. The consistency of the pattern from date to date further indicates that larvae were not dispersing to the west and south shores to any large extent. Second, the south shore apparently was utilized primarily by larvae from an earlier hatching series as evidenced by the length distribution data in Figs. 7 and 8. We do not know if these larvae hatched in this area (SS I) or dispersed to it later from another area. Apparently very few larvae from the May hatching series utilized the south shore area. Third, although larval lake herring were nearly always more abundant in the 0-2 m stratum than in the 4-6 m stratum, at times they did occur in substantial numbers at 4-6 m along the north shore. Only rarely were they present in this depth stratum along the west and south shores.

There is some slight evidence that in June larvae moved away from the west end of the lake to deeper water. On 11 and 18 June 1982 nearly all larvae collected were in zones NS II and SS II and in the open water between these zones (Figs. 11 and 12).

In general the vertical pattern of distibution was what we expected based on the studies previously mentioned. We need additional sampling to fully characterize the horizontal distribution. The 1982 data clearly indicate that the nearshore area around the Duluth Entry and along the northshore is a very important high-density area. The 1981 data suggest that this high-density area extends out from the west- and northshores into deeper water, but exactly how far we do not know. It probably does not extend much further east than the Lester River nor much further south than the Superior Entry. The density in Duluth Entry area freqently exceeded 1000/1000 m and was 10 to 100 times higher than densities along the west and south shores.

We were unable to sample in areas much less than 5 m deep, and it may be that larvae were even more dense in these areas. Pritchard (1930), Faber (1970), and Clady (1976) all report large numbers of lake herring larvae in very shallow water near shore. Clady attributes this nearshore aggregation to active movement by the larvae. The 1981 and 1982 data taken together suggest that prior to emigration in middle June larval density decreases rapidly with distance from the shoreline. Any further quantitative sampling will have to include shallow-water sampling as well as more deep-water sampling so that a clearer picture of horizontal distribution can be obtained.

GROWTH AND MORTALITY ESTIMATES

We had not intended to estimate growth and mortality rates

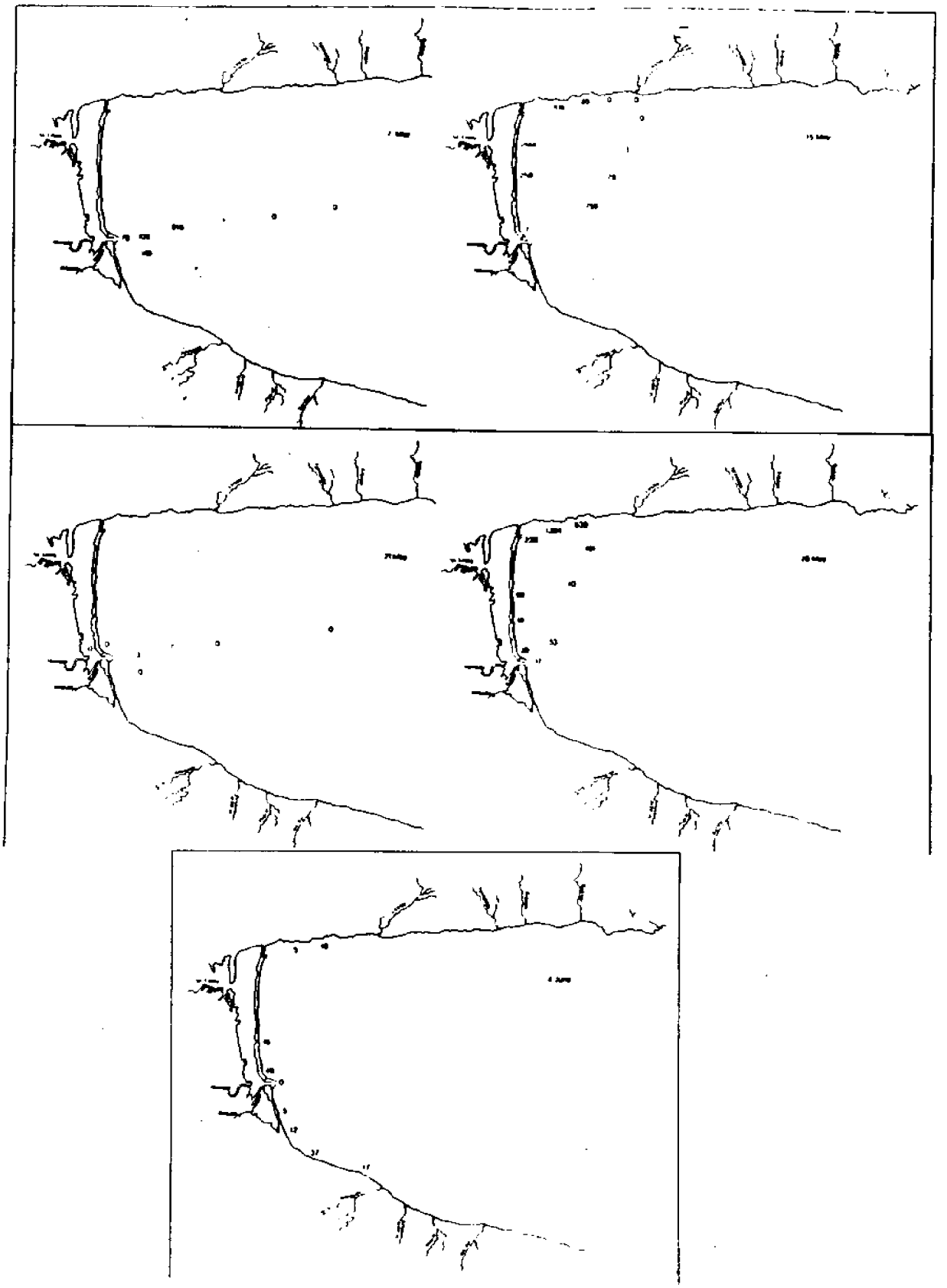

Figure 6. Mean CPE (no./1000 m) of lake herring larvae at each sampling station, 7 May - 4 June, 1981.

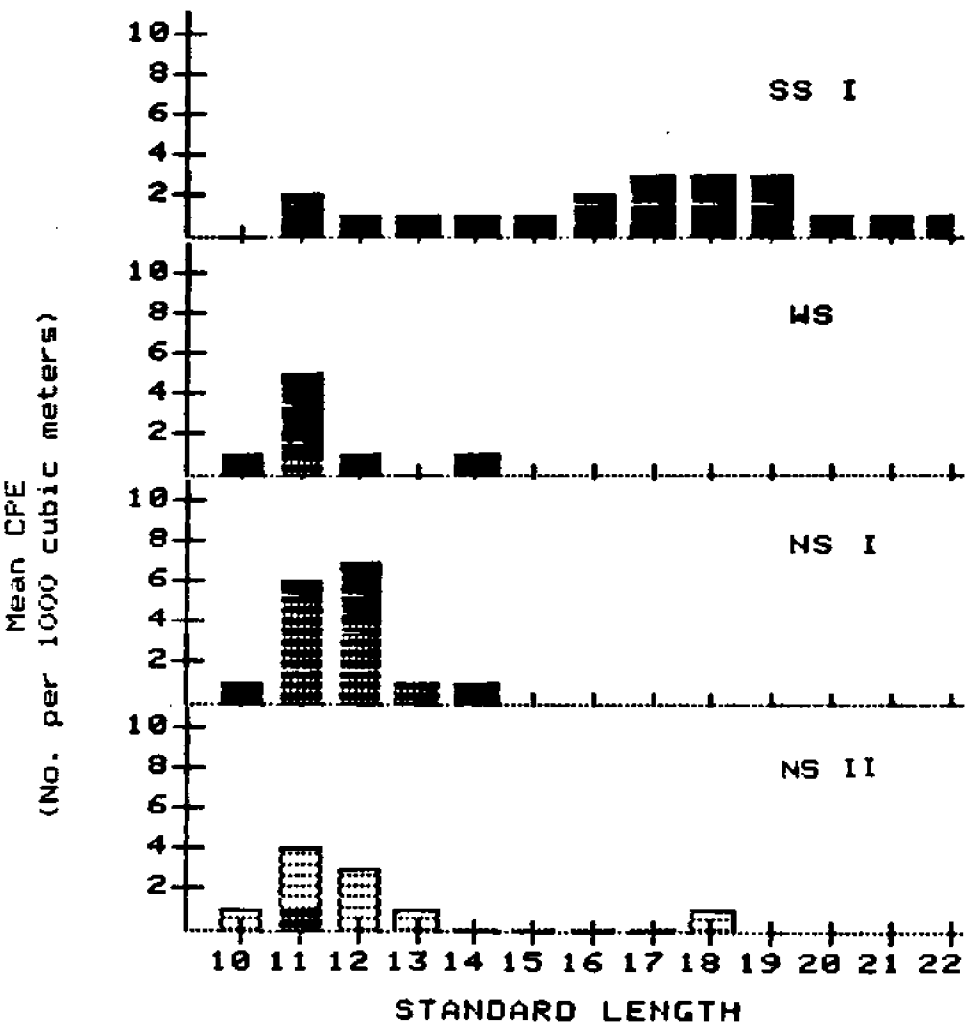

Figure 7. Size-specific distribution of larval lake herring captured in western Lake Superior on 7 May 1982. (0-2 m depth stratum denoted by solid part of bars; 4-6 m depth stratum denoted by dotted portion of bars).

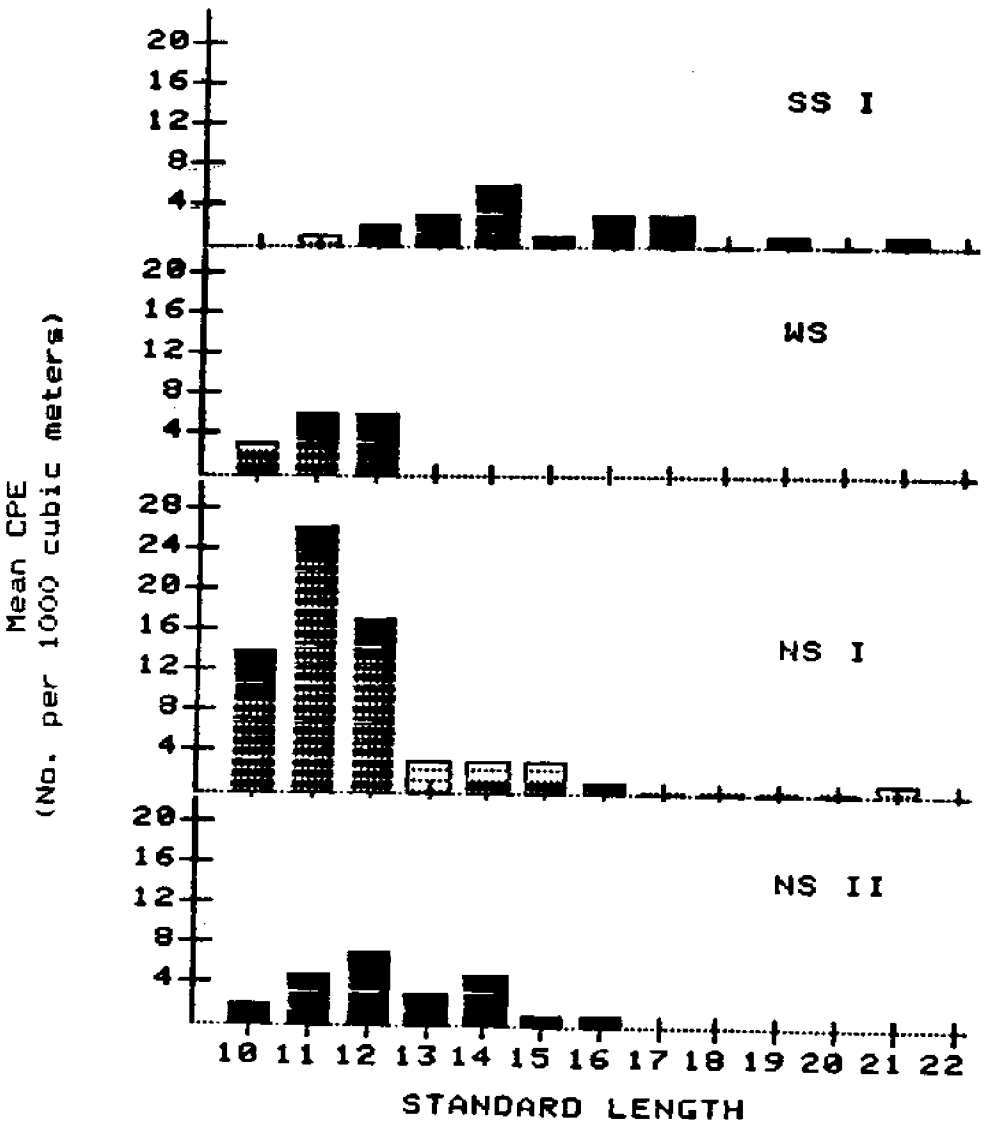

Figure 8. Size-specific distribution of larval lake herring captured in western Lake Superior on 14 May 1982. (0-2 m depth stratum denoted by solid part of bars; 4-6 m depth stratum denoted by dotted portion of bars).

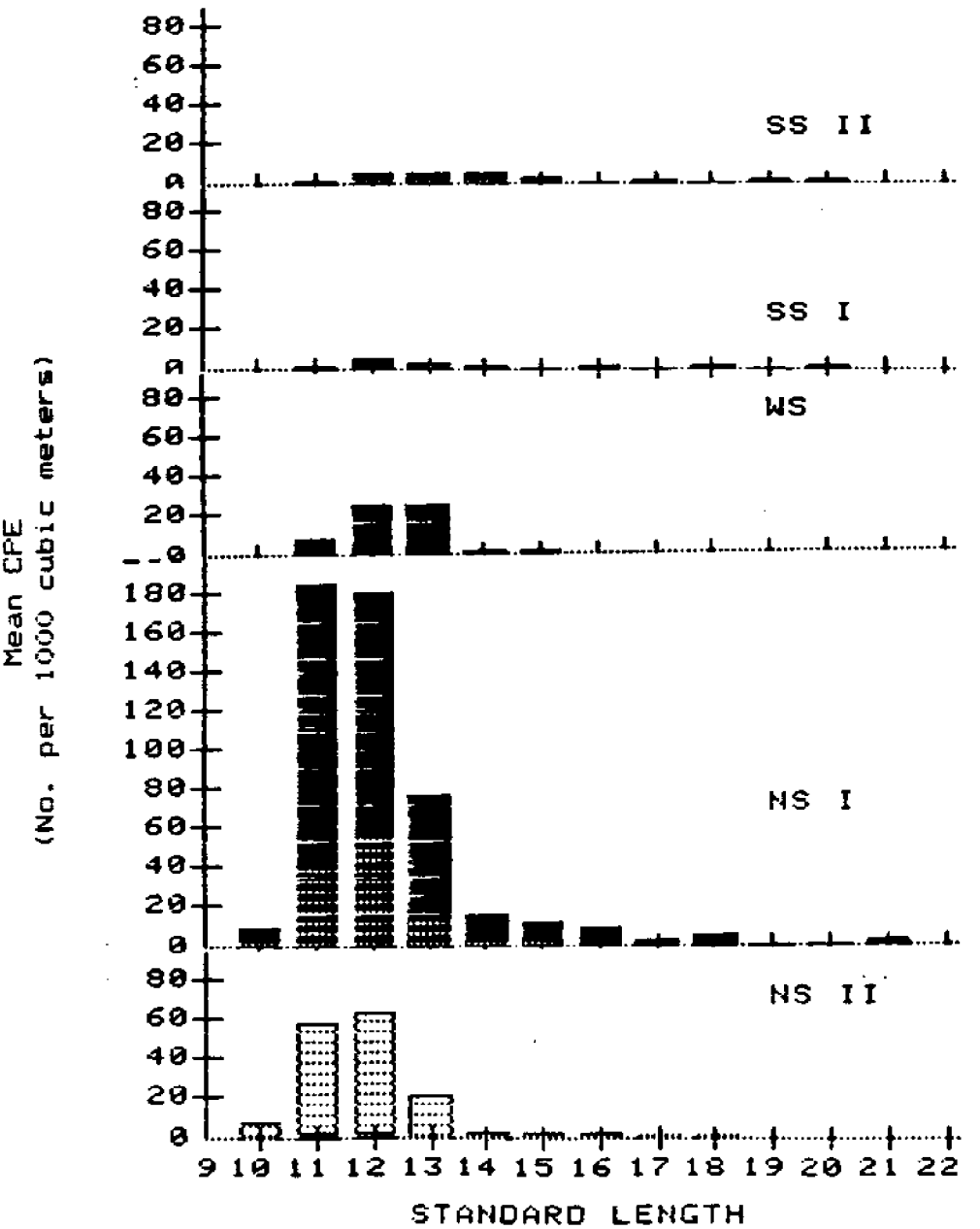

Figure 9. Size-specific distribution of larval lake herring captured in western Lake Superior on 24 May 1982. (0-2 m depth stratum denoted by solid part of bars; 4-6 m depth stratum denoted by dotted portion of bars).

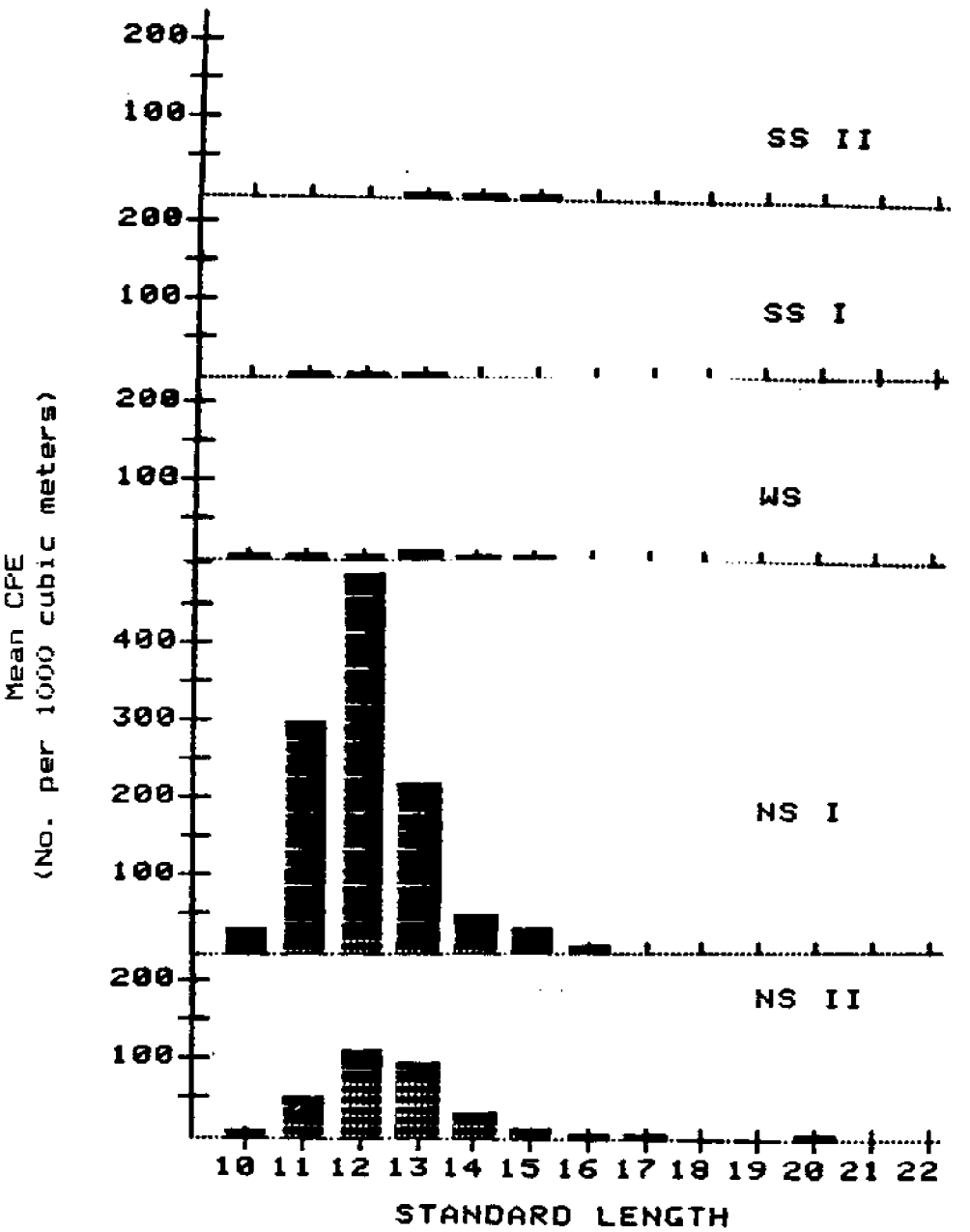

Figure 10. Size-specific distribution of larval lake herring captured in western Lake Superior on 28-30 May 1982. (0-2 m depth stratum denoted by solid part of bars; 4-6 m depth stratum denoted by dotted portion of bars).

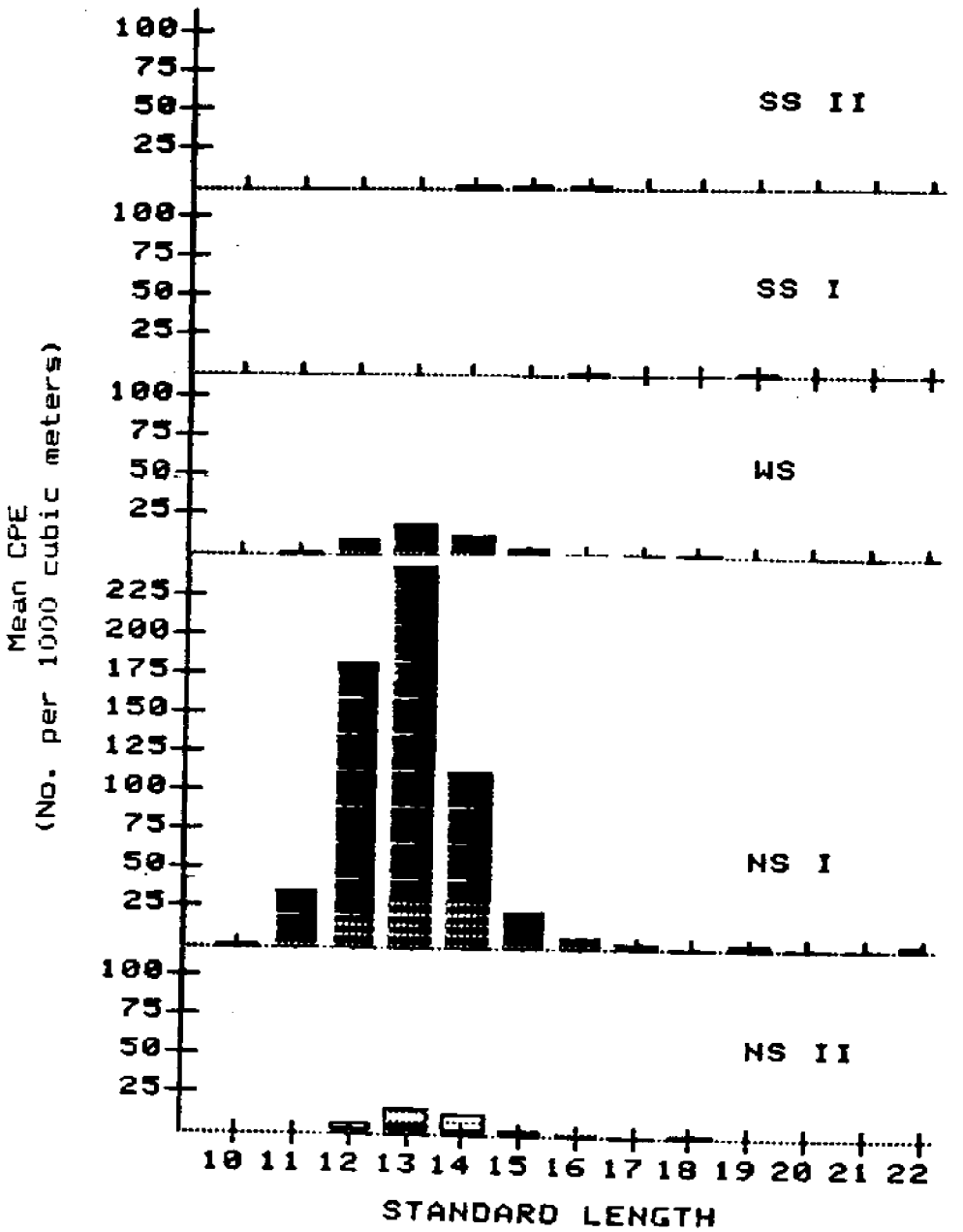

Figure 11. Size-specific distribution of larval lake herring captured in western Lake Superior on 3 June 1982. (0-2 m depth stratum denoted by solid part of bars; 4-6 m depth stratum denoted by dotted portion of bars).

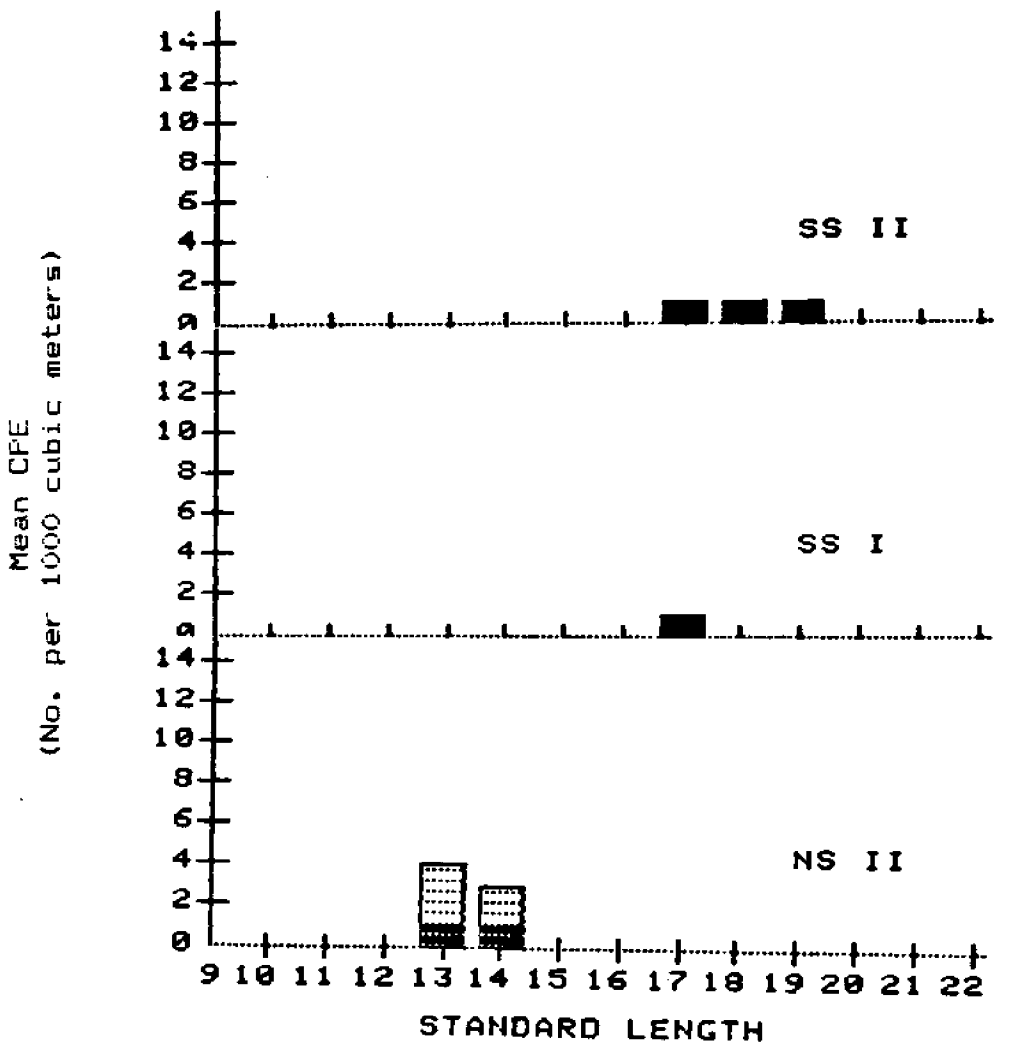

Figure 12. Size-specific distribution of larval lake herring captured in western Lake Superior on 11 June 1982. (0-2 m depth stratum denoted by solid part of bars; 4-6 m depth stratum denoted by dotted portion of bars).

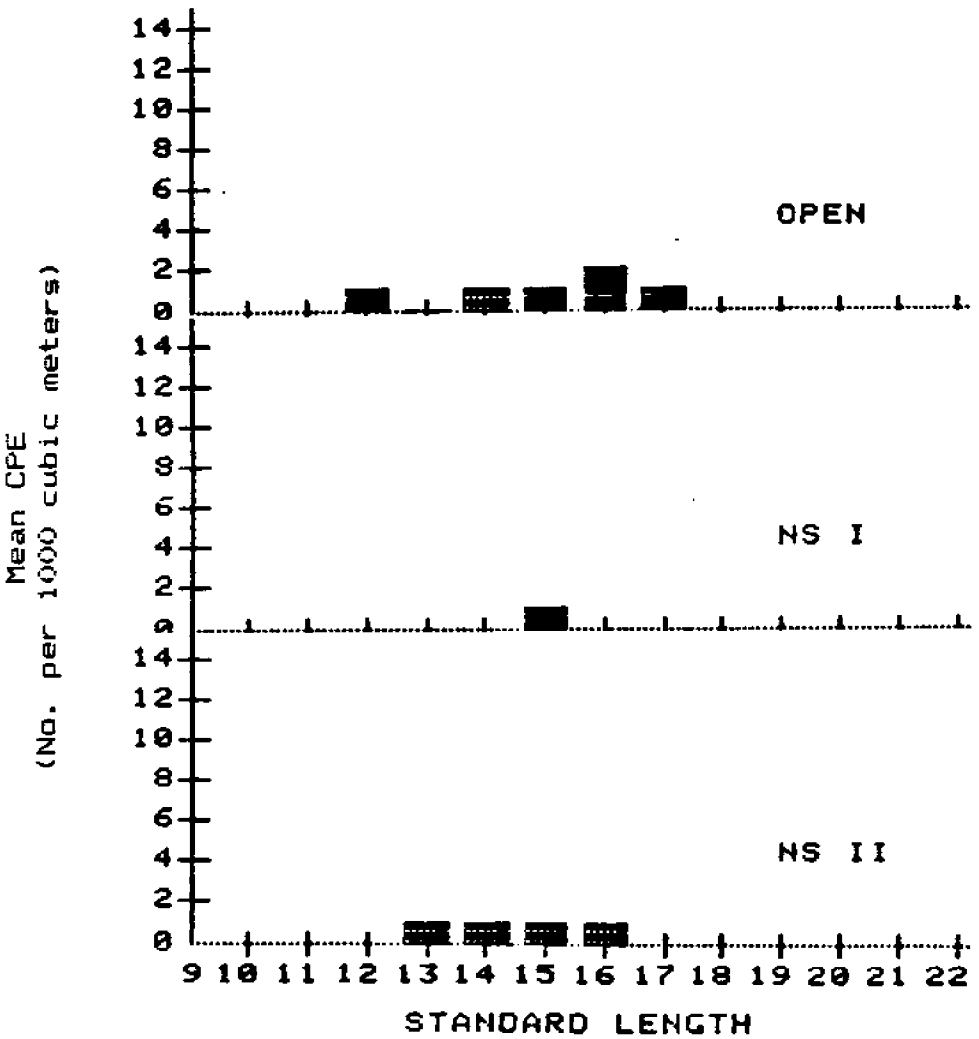

Figure 13. Size-specific distribution of larval lake herring captured in western Lake Superior on 18 June 1982. (0-2 m depth stratum denoted by solid part of bars; 4-6 m depth stratum denoted by dotted portion of bars).

from the 1981 and 1982 data since these data were collected primarily to answer questions about how, when and where to sample. However, since the project was not continued, we decided to attempt preliminary estimates of instantaneous growth rates using the methods of Hackney and Webb (1978). After plotting the 1981 mean CPE for each length group against sampling date to determine the dates on which an average individual attained a given length, it was apparent that our data would not yield reasonable results for larvae smaller than 11 mm SL and larger than 16 mm SL. We began sampling too late to adequately sample the smaller larvae, and we did not capture enough larger larvae to make reasonable plots. However, for larvae between these lengths we computed the following exponential growth curve (ln-transformed): $\ln L = 2.293 + .0.0545 t$ ($r = 0.994$), where L is the standard length in mm and t time in days ($G = 0.0545$).

From this equation we determined the age of each length group between 11 and 16 mm SL. Although we used whole number, 1-mm length groups in our graphs, the actual midpoint lengths were used in all calculations. The midpoints were: 10.60, 11.75, 12.70, 13.80, 14.85, and 15.90. After the age in days had been assigned to each of these midpoints, we plotted the natural logarithm of cumulative CPE (the area under a mean CPE x sampling date plot) against age to give a larval catch curve. The slope of this curve was -0.4110 ($r = 0.994$), which means that the instantaneous mortality rate Z has the value of 0.4110 when age is expressed in days.

A rather similar estimate of Z was obtained when a grand average of CPE was used instead of cumulative CPE. The Z value of this catch curve was 0.4176 ($r = 0.992$).

We attempted one more set of calculations based on the 1982 catch data from zone NS I, the zone of highest density throughout May and early June. From these data we calculated a $G = 0.0543$ ($\ln L = 2.320 + 0.0543 t$; $r = 0.974$). A catch curve based on cumulative CPE yielded $Z = 0.5837$ ($r = 0.970$), while one based on grand average CPE yielded $Z = 0.5931$ ($r = 0.958$).

The growth rate estimates from the 1981 and 1982 data agree rather closely with each other, but we believe that they are overestimates. If we use the 1982 data to calculate average daily growth increment during the first week after hatching, we get a mean of 0.69 mm/day. Anderson and Smith (1971) reported increments of 0.13-0.63 mm/day (converted from average weekly increments) for C. artedii larvae reared from stock from the Duluth-Superior area. Their larvae grew to 37.5 mm TL under simulated lake temperatures (6.1-10.5 C). The grand average increment was 0.27 mm per day. Table 1 indicates that our specimens probably experienced similar or slightly lower temperatures, and thus it seems unlikely that they would have grown 0.69 mm/day, especially during their first week. Hinrichs

(1979) does not report weekly or daily increments for the C. artedii that he reared, but calculations from his data yield consistent values of 0.25 mm/day during the first 16 days. These larvae were reared at temperatures of 9.9-13.0 C, which are close to the optimum growth temperatures reported for this species by McCormick et al. (1971).

It is still possible that the field specimens could have grown faster than reared specimens if quality and quantity of food was low for reared specimens. Exogenous nutrition is extremely important for good growth even during the yolk sac phase (John and Hasler 1956). The specimens that we reared fed poorly, and their average daily increments during the first week were 0.08-0.13 mm, with a grand average of 0.11 mm. The highest incremental growth rate determined for any individual was 0.23 mm/day for a 32-day larva (using 10.0 mm SL as a mean size at hatching). When length ranges of our field and hatchery specimens are compared at similar stages of development, it is clear how much growth rate can be affected by food availability (Table 6).

If we compare our incremental rates from the field with those of other field estimates, ours still seem high. Clady (1976) reported a value of 0.6 mm/day for Oneida Lake lake herring larvae, but this was an average over a size range of 11-21 mm TL and also included data from 6 years. Oneida Lake is also much warmer and much more productive than Lake Superior. Growth conditions in the Bay of Quinte, Lake Ontario, are also more favorable than those of Lake Superior, and lake herring larvae there showed an average daily increment of 0.58 mm during a 7-day period in early May. We calculated this value from mean lengths of specimens captured each day as reported by Pritchard (1930). However, Pritchard also reported that 16 mm TL larvae were about 20 days old. Since his newly hatched specimens averaged 10 mm TL, the daily increment would be 0.3 mm.

It is clear from the size-specific catch data in both years that we under sampled newly hatched larvae (10 mm SL). Such under representation in the catch would contribute to an underestimation of age and, thus, an overestimation of growth rate. The same bias would lead to an underestimation of mortality rate. However, the loss of larger larvae from the catch due to emigration probably overcompensated for this bias and gave us an unrealistically high mortality rate. Rates calculated for other freshwater larvae have been below 0.3 (Hackney and Webb 1978; Dahlberg 1979; Cada and Hergenrader 1980).

The ages that we determined for 1981 and 1982 larvae between 11 and 16 mm SL were similar in, as the similar growth rates suggest. We assigned ages of 6.97 - 8.49 days for larvae in the 14.85 (15) mm SL length category. For the reasons discussed above, we believe that these larvae were somewhat

Table 6. Size comparisons of wild-caught and reared larval lake herring at similar stages of development. Wild-caught larvae from western Lake Superior, 1981-82.

Developmental stage	Size Range (SL mm) Wild-caught	Reared	Age Range of Reared Larvae (days)
Early Protolarvae	8.8 - 12.2	9.5 - 11.9	0 - 6
Late Protolarvae	11.5 - 14.3	10.3 - 12.4	7 - 9
Early Mesolarvae	12.6 - 17.2	10.8 - 14.0	10 - 21
Mesolarvae II	14.0 - 21.0	13.3 - 17.5	21 - 39
Mesolarvae III	19.1 - 22.4	15.3 - 18.3	43 - 61

older than this. From the data in Table 6, which compares developmental stages of our wild-caught and reared larvae and associates them with age, and from comparisons with the studies cited above, we estimated that on the average lake herring larvae spent about 14-20 after hatching in the study area. During this time they reached the middle to late mesolarval stage of development (mesolarva II or III) and attained sizes of 17-22 mm SL.

CONCLUSIONS

Although this was a preliminary study, we feel justified in drawing the following tentative conclusions. First, we believe that the north shore area in the vicinity of the Duluth Harbor Entry is an important developmental area for lake herring in western Lake Superior. A rather large number of larvae apparently hatch in this area and remain there through all of the protolarval phase and most of the metalarval phase. We do not have a total abundance estimate, but the densities measured in this area were unexpectedly high. Sampling closer to shore may well reveal even higher densities in future.

Second, we believe that the Duluth-Superior area of western Lake Superior offers excellent potential for developing index stations for measuring larval relative abundance. Reckan (1978) has demonstrated the utility of using larval abundance estimates from index stations for predicting subsequent year-class strength in lake whitefish (Coregonus clupeaformis). If it can be shown that larval abundance is a reliable predictor of year-class strength or if it can be shown that it is a reliable predictor under certain conditions, fishery managers will be able to estimate the status of recruitable stocks 3 to 4 years sooner than it is now possible. Because lake herring larvae congregate in the Duluth-Superior area, they are relatively easy to sample in replicate. Thus, it should be possible to develop fairly precise estimates of larval density with relatively little effort.

Third, we believe that reasonably accurate estimates of growth and mortality rates also can be determined. The estimates can be improved greatly by increasing the catch efficiency of newly hatced larvae. This can be done by including sampling stations closer to shore and by sampling more often. Even though our growth rates are probably overestimates, they still indicate that 7-day sampling intervals are too long. Mortality estimates can be improved both by more accurate growth estimates and by sampling so that some estimate of emigration from nearshore to deeper water can be made. Even if accurate estimates are not possible, precise, systematic estimates from year to year would allow biologists to assess what extrensic factors lead to good relative growth and low mortality in larval populations.

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