FRED Reports

LIMNOLOGICAL AND FISHERIES EVIDENCE
FOR REARING LIMITATION OF
SOCKEYE PRODUCTION
IN CRESCENT LAKE, SOUTHCENTRAL ALASKA
(1979-1982)

by
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Number 57

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Don W. Collinsworth
Commissioner

Stanley A. Moberly
Director

P. O. Box 3-2000
Juneau, Alaska 99802

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PART I: Crescent Lake Fisheries Program

by

Gary B. Kyle

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ABSTRACT

In order to apply the appropriate sockeye salmon, *Oncorhynchus nerka*, enhancement strategy at Cresent Lake, an assessment was made of the fisheries and limnological conditions that determine successful rearing of juveniles to smolt. We have utilized a two-tier approach that specifically addresses fishery ecology (Part I) as one tier and limnetic production patterns (Part II) as the second.

Of the estimated 2,011,855 smolts that migrated from Crescent Lake in 1981, a majority (72%) were small age-1.0 fish, averaging 68 mm in length and 2.8 g in weight. In contrast, 471,768 smolts were estimated to have migrated from the lake in 1982; however, a majority (nearly 60%) required two years of freshwater rearing before emigrating. In addition, age-1.0 smolts were small, averaging 69 mm in length and 2.7 g in weight. Parent-year escapements for the age-1.0 smolts (indexed by sonar counters) equalled 87,000 adult fish in 1979, compared to 91,000 spawners in 1980 and 41,000 in 1981. Finally, 70% of the adult fish entering the lake had spent 3 years in the ocean in 1979 compared to 89% in 1980 and 82% in 1981.

Crescent Lake is oligotrophic; its open-water period lasts five months, beginning in mid-June. Surface temperatures characteristically reach 10° to 12° C for short periods. Compared to 9 and 10 m in both the spring and fall, the light-compensation depth was reduced to 4 m by the midsummer intrusion of turbid glacier meltwater. Total phosphorus (TP) levels rose from premelt minimal levels of 4 $\mu g\ L^{-1}$ to peak levels of 10 $\mu g\ L^{-1}$, during the mid-August height of the turbid inflow. As the principal component of the TP imported into the epilimnion consisted of particulate inorganic forms, algal response (chl a) lagged 2-3 weeks behind the peak TP input, reaching 5.20 mg/m^3 to 1.71 mg/m^3. In contrast, as a consequence of reduced volumetric uptake combined with a shallowed photic zone, areal carbon uptake was reduced during the period of high turbidity. Finally, the primary forage available to sockeye fry consisted of the macro-zooplankter *Cyclops scutifer*, which reached maximal densities in mid-August as small-body-sized (<0.70 mm) pre-adults. Large-body-sized (≥0.85 mm) adult copepods appeared briefly in the spring, when the mean body size of the zooplankter population exceeded 1.00 mm.

In summary, the sockeye smolt population characteristics of threshold size and extended freshwater age argue for an insufficient freshwater rearing environment. The oligotrophic nature of the lake that is exacerbated by the midseason inflow of cold, turbid glacial meltwater, and the total exclusion of preferred forage species (cladocerans) limits production for sockeye smolts.

KEY WORDS: Limnology, glacial, sockeye salmon, *Oncorhynchus nerka*, smolt, phosphorus, lake fertilization, lake enrichment, euphotic zone, turbidity, hydroacoustics, silt, nutrient loading

INTRODUCTION

For nutrient enrichment to lead to an increased fertility within salmon nursery lakes, the level of available nutrients (seasonal loading to the surface strata) must be limiting to primary production. Moreover, in order for the lake rearing of sockeye salmon, *Oncorhynchus nerka*, to benefit from increased freshwater fertility, the in-lake residence period must be limiting to smolt production. Such limitations may be expressed as poor freshwater growth leading to decreased in-lake fry survival (Burgner 1964; Johnson 1965; Narver 1966); increased in-lake residence time, i.e., age-2.0 to 3.0 smolts (Krogius 1951, 1961; Foerster 1968); and/or the production of minimal-sized (threshold) smolts (Ruggles 1965; Koenings et al. 1984, 1985). Thus, by increasing the fry growth rate through enhancing the rearing environment, a greater biomass (number and individual weight) of age-1.0 smolts can be achieved. In turn, a greater smolt biomass is consistent with the increased production of adult fish available to the common property fishery (Krogius 1951; Foerster 1968; McAllister et al. 1972; Hyatt and Stockner 1985).

In order to determine the effect of in-lake juvenile growth patterns on smolt production, the Fisheries Rehabilitation, Enhancement, and Development Division (FRED) of the Alaska Department of Fish and Game (ADF&G), as part of a comprehensive prefertilization evaluation of Crescent Lake enumerated the sockeye smolt emigration in 1981 and 1982. In addition, smolt size, age composition, and migration timing were determined. Moreover, in order to specifically manage the Crescent Lake sockeye salmon stock, the Commercial Fisheries Division of the ADF&G began monitoring the adult fish returns in 1979 to determine (1) magnitude of the escapement, (2) migrational timing, (3) stock composition of the sockeye harvest in the commercial fishery, and (4) age, length, sex, and scale characteristics.

The purpose of this report is to present the results from these fisheries projects and surveys that characterize the production of sockeye salmon from Crescent Lake. The fisheries assessment and the limnological considerations will determine the potential for implementation of a nutrient-enrichment program.

Study Site Description

The Crescent River drainage, which is located on the west side of central Cook Inlet and directly north of Tuxedni Bay (Figure 1), encompasses 300 km^2, including the 1,647 ha of Crescent Lake. This semiglacial lake is approximately 10 km long and 3 km wide; it has an average depth of 23 m. The Crescent system contains all five species of Pacific salmon; however, sockeye salmon is the primary one.

MATERIALS AND METHODS

Juvenile Sampling

Townet sampling for juvenile sockeye salmon was conducted in Crescent Lake on 25 September 1979. The objective of this sampling was to determine the age, length, weight, relative abundance, and distribution of rearing juvenile sockeye salmon. Detailed methods are discussed by Barton (1974) and Waltemyer (1976); however, a standard 2.7-m-wide by 2.7-m-deep by 3.2-m-long Burgner townet (Burgner and Green 1963) was used to sample 10 stations. Surface tows were made approximately 61 m behind the boat at a velocity of approximately 1.2 m/sec. As such, a 20-minute tow resulted in the sampling of approximately one surface acre of water.

A minimum of 300 juvenile sockeye salmon were preserved in 10% formalin for analysis of age, weight, and length. A scale smear

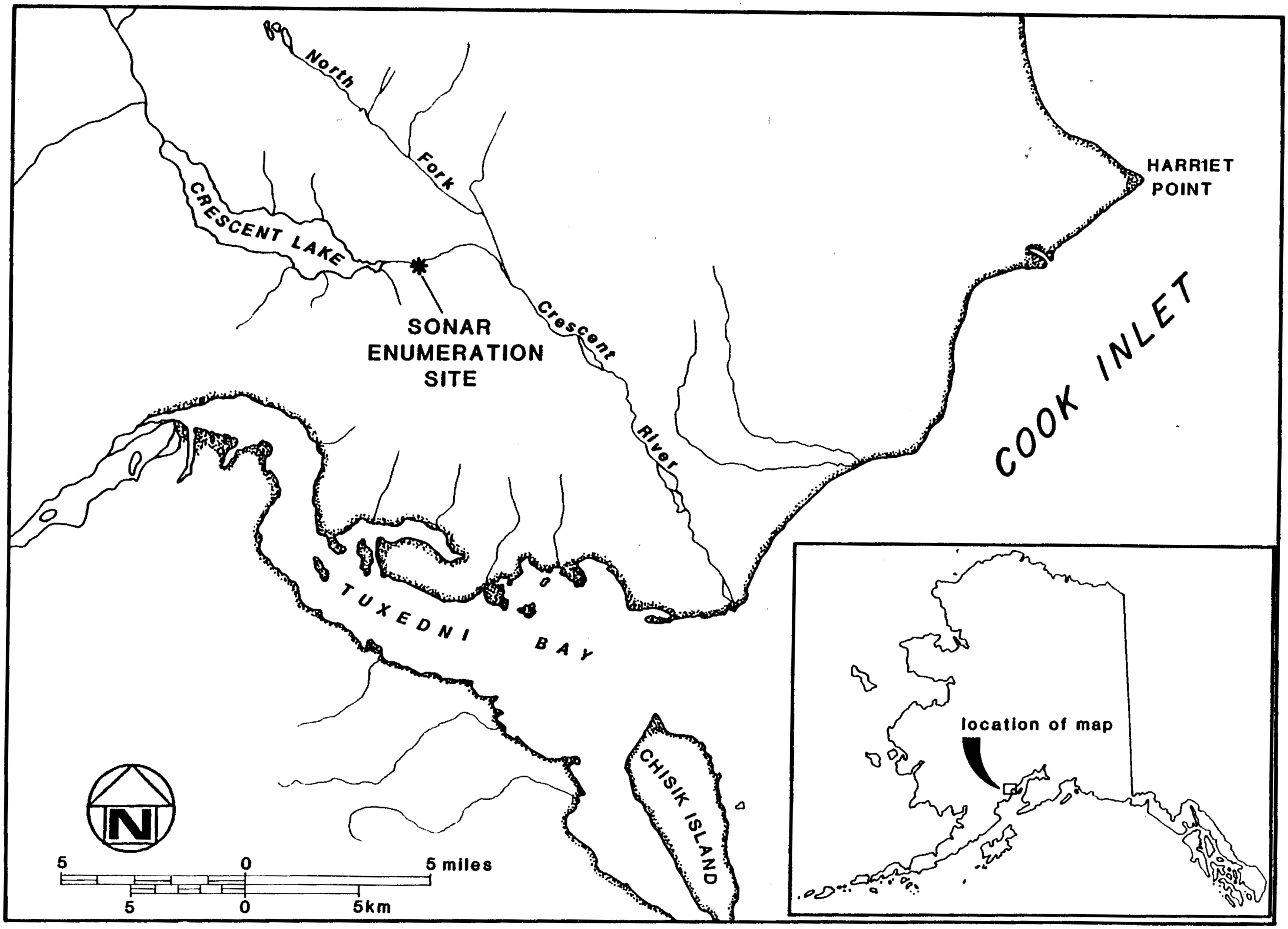

Figure 1. Map showing the Crescent River drainage system and location of the adult sonar enumeration site.

was taken from the primary scale-growth area (Scarnecchia 1979), mounted between two glass slides, and analyzed for age using a Microfische projector. Snout-to-fork lengths were measured to the nearest millimeter; weights, to the nearest 0.1 g.

Smolt Enumeration and Sampling

Migrating sockeye salmon smolts were captured in Crescent River during 1981 using two fyke nets (0.95 cm mesh); each measured 1.2 m wide by 1.2 m deep with 7.6-m wings (Figure 2). A 0.9- x 1.5- x 1.1-m live-box was attached to the cod-end of each net. The nets were suspended from a 0.95-cm cable stretched across the river and were placed adjacent to each other in the middle of the river. The combined sampling area of the nets represented 34.2% of the linear width and 17% of the cross-sectional area of Crescent River. Because of the movement of lake ice down the river between 19 May and 19 June, the nets were consistently fished only between 2000-0100 h. However, when possible, sampling was conducted to determine diel migration. Thereafter, the nets were fished continuously until the end of the project on 7 July.

Because of the the great effort involved in cleaning the fyke nets in 1981 and the need to stabilize catch efficiency, in 1982 migrating sockeye smolts were captured using five incline-plane traps. The frames of the traps were constructed of angled aluminum; vexar plastic netting covered the sides, and perforated aluminum plates were placed on the bottoms in a tapered-folded design (Figure 3). The V-shaped troughs provided for maximal water flow-through and minimal debris and smolt impingement, but most importantly, they were designed to eliminate a pressure wave in front of the traps so that smolts were less likely to avoid capture. A live-box attached to the end of each trap was also constructed of angled aluminum; it had perforated aluminum plate on the sides and plywood on the bottom and back panels (Figure 3). When the

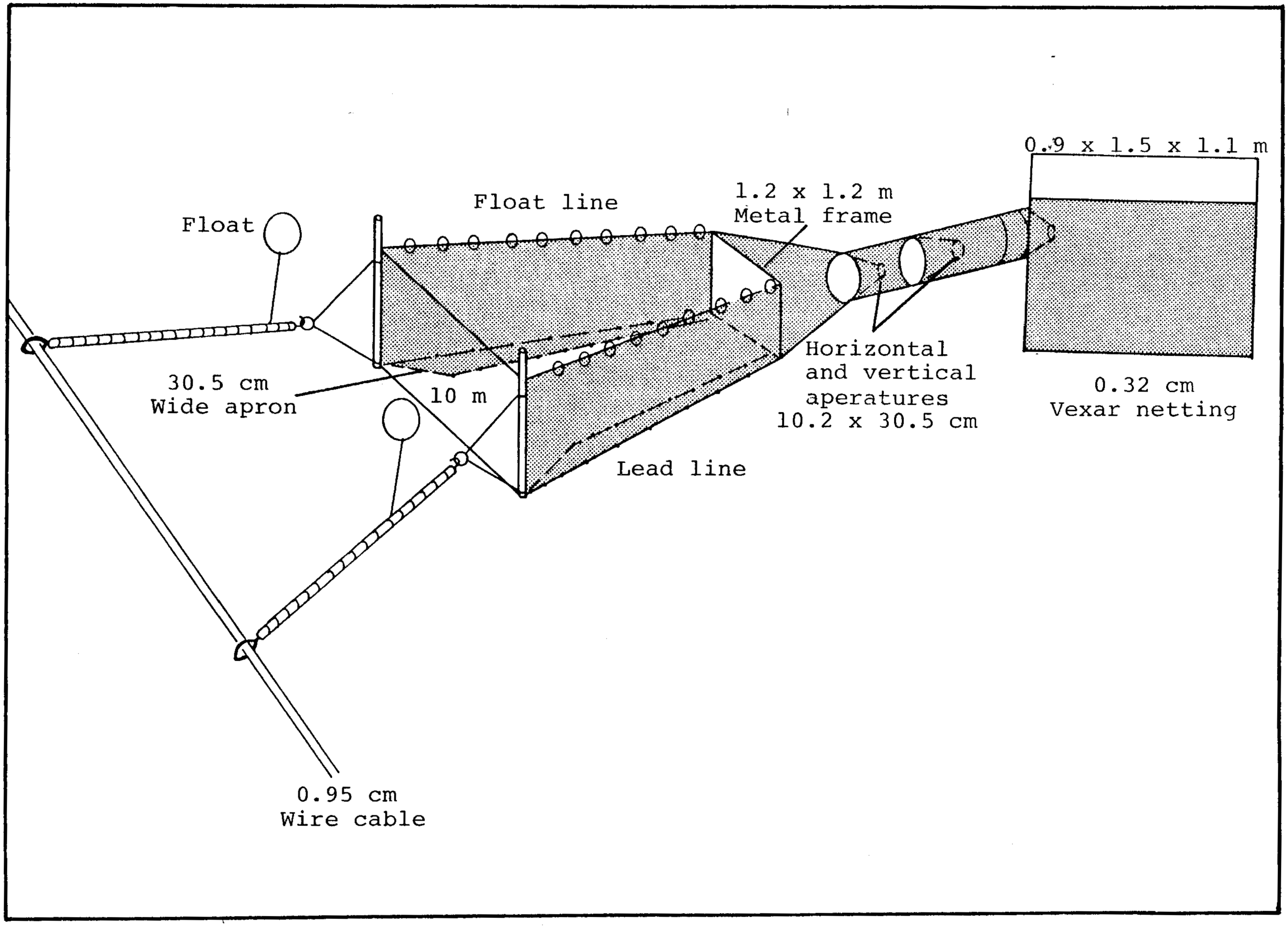

Figure 2. Fyke net and live-box design used to sample smolts in Crescent River, 1981.

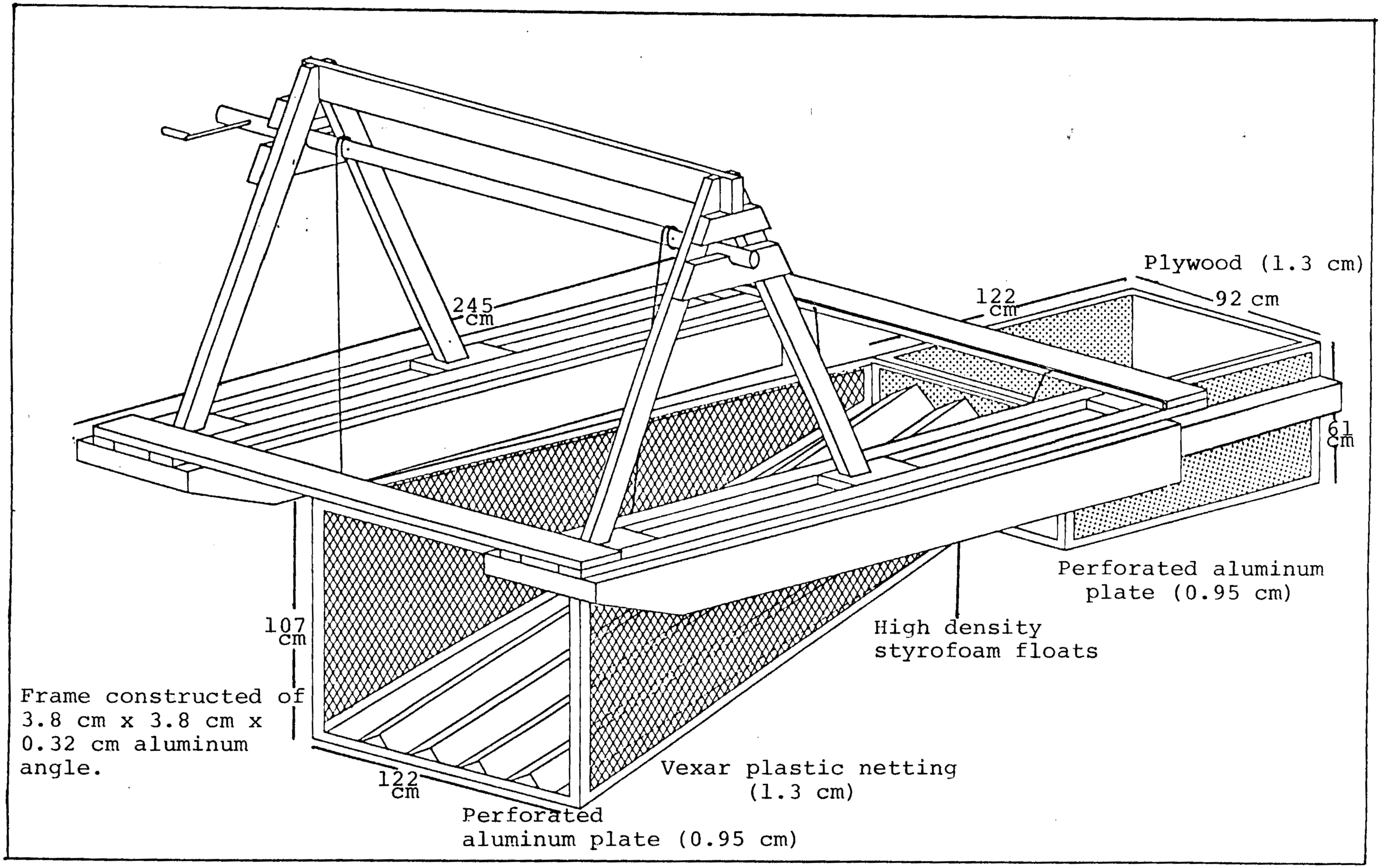

Figure 3. Diagram of incline plane traps used to capture sockeye smolts in Crescent River, 1982.

water velocity became too great to lift the traps out of the river by hand, a saw-horse structure (constructed of a wood frame with a hand-crank attachment) was used to remove the traps.

The traps were suspended from a 0.95-cm-diameter cable stretched across and above Crescent River at a location that was 19.5 m wide (Figure 4). The traps sampled the upper 1-m depth of water and a linear width of 6.1 m, or 30% of the total. The cross-sectional area sampled varied with fluctuating discharge; however, the average area sampled was 12%. The traps were sampled continuously from 24 May until 6 July. All fish captured were identified by species and enumerated four times a day (2000 h, 0200 h, 0800 h, and 1400 h). On several occasions the traps had to be removed or relocated because of drifting ice and increasing water velocity or for operational adjustments. On 1 June traps 3 and 5 were swept downstream by ice floes and, consequently, slightly damaged. As a result of increasing velocity and drifting ice, the traps were moved on 2 June to an upstream site where the velocity was slower. However, the catch efficiency was severely reduced, because the slower velocity allowed smolts to avoid the traps. Thus, the traps were relocated on 5 June to the original site. Finally, on 15 June a vertical gill net (1.5 m x 3.0 m x 9.5 mm stretch measure) was suspended below trap 1 and 5 (Figure 4) for two hours; it indicated that smolts were migrating under the traps. As a result, the floats of each trap were removed and covered with burlap (in the front and on the bottom) in an attempt to eliminate trap avoidance. Other trap-avoidance evaluations (gill-netting below the traps) were conducted on 17 and 20 June.

If $\leq$1,000 sockeye salmon smolts were captured in one day, scale samples and length-weight measurements were collected from 20 smolts; if 1,000-3,000 were captured, they were collected from 30; if 3,000-5,000 were captured, from 40; and if more than 5,000 smolts were captured each day, from 50. The mean length and weight and

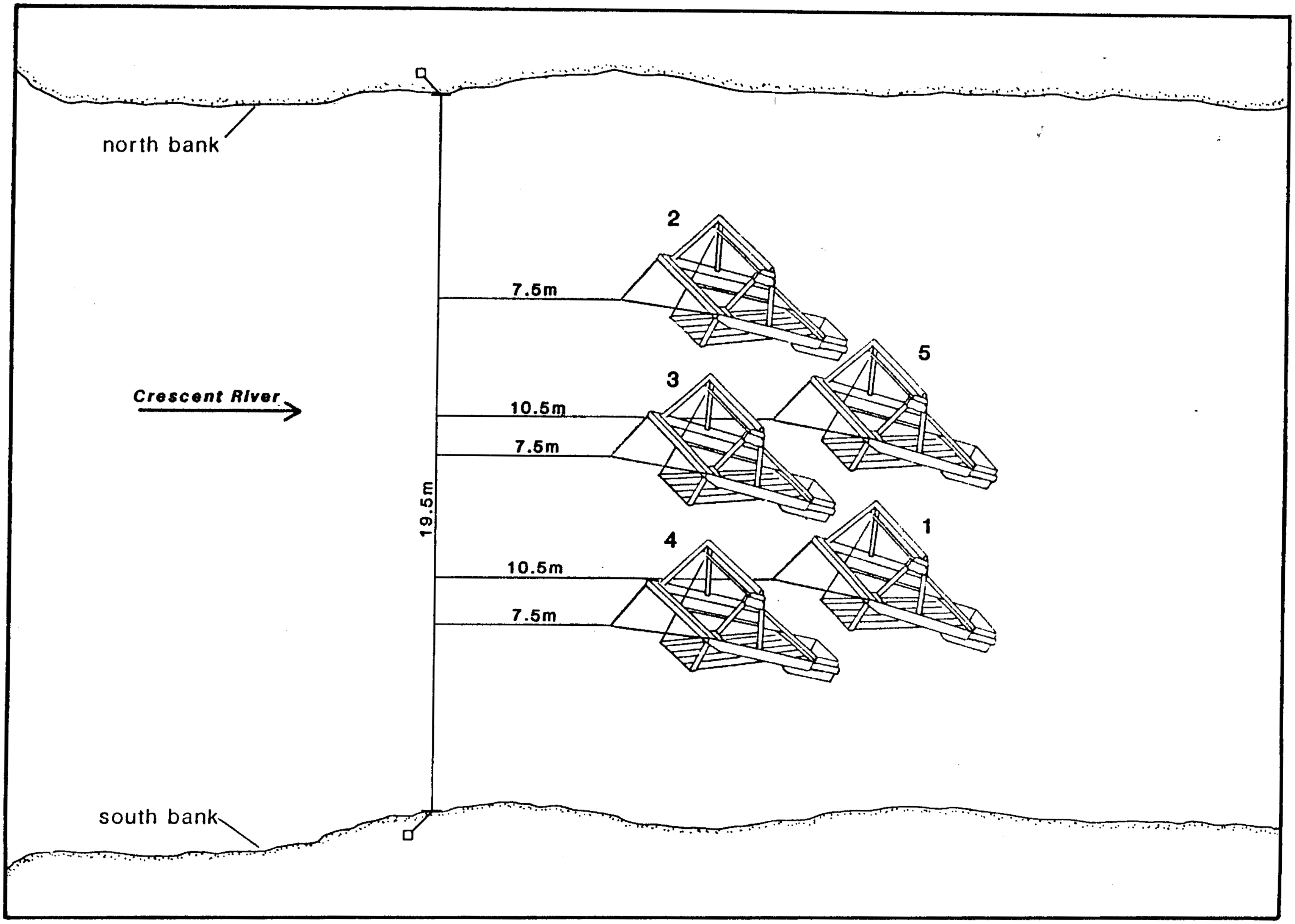

Figure 4. Arrangement of the five incline plane traps used to capture sockeye smolts in Crescent River, 1982.

age-class distributions were weighted according to the relative magnitudes of the smolt out-migrations during the weekly sample period (Cochran 1963). Scales were taken from the primary scale-growth area (Scarnecchia 1979) and placed on glass slides for later age analysis (Koo 1962). Smolts were anesthetized with MS-222, measured for fork length to the nearest millimeter, and weighed to the nearest 0.1 g.

The catch efficiency of the nets and traps was determined by weekly mark and recapture analyses. Each week 200-500 smolts were placed in an aerated tank containing a solution of Bismark Brown dye (1:30,250 w/w) for one hour. The dyed smolts were then transported to a riffle area in Crescent River, approximately 1.0 km upstream of the traps, and evenly distributed across the river.

The weekly total number of migrating smolts was estimated by the method described by Rawson (1981):

$$\hat{N} = n \frac{D}{d} \left[1 + \frac{D-d}{Dd} \right].$$

Where D was the number of individuals marked and released during the first mark-recapture experiment; n was the number of unmarked individuals captured before the next mark-recapture experiment; d was the number of marked individuals recaptured before the next mark-recapture experiment; and N was the estimated total number of migrating smolts. The variance (V) of the estimator, ($\hat{N}$), was as follows:

$$V(\hat{N}) = n(n+d)D \frac{D-d}{d^3}.$$

Then, assuming N followed a normal distribution, the confidence interval (CI) was as follows:

$$95\% \text{ CI} = \hat{N} - 1.96 \sqrt{V(\hat{N})} \text{ to } \hat{N} + 1.96 \sqrt{V(\hat{N})}$$

Weekly total numbers of migrating smolts were summed to obtain the estimated sockeye smolt population. The sum of the variances for each weekly estimate was used to compute the overall confidence interval for the sockeye smolt population estimate.

Physical parameters, including river stage height, mean water temperature, precipitation, and light measurements (1982) in Crescent River, were taken daily. At the smolt sampling site, river stage heights were measured in meters with a Stevens staff gauge. Water temperatures were measured with a calibrated Taylor maximal-minimal recording thermometer. Precipitation measurements were recorded in centimeters, using a Taylor rain gauge. Light penetration was measured in Crescent River with a Protomatic submersible photometer, and the measurements were expressed as percent of incident light at 0.3-m-depth intervals from surface to the bottom.

Adult Enumeration and Sampling

Since 1979 returning adult sockeye salmon to Crescent Lake have been indexed in Crescent River near the outlet (Figure 1). Index counts for other salmon species in Crescent River are lacking, because the counting site is upstream of major spawning areas. However, in 1979 escapement apportionment (past the sonar site) for each species was based on seine catches. The sonar counters were installed at the end of June and were removed at mid-August of each year.

Adult sockeye salmon were collected from Crescent River by seine and gill net in 1979 and 1980 and by seine and fishwheel in 1981 to obtain length, weight, sex, age, and scale-pattern information. At least 500 adults each year were sampled from the escapement. Lengths (mid-eye to fork) and weights were measured to the nearest 0.5 cm and 0.1 kg, respectively. Age and scale-pattern analyses were conducted by the ADF&G Commercial Fisheries Division stock-separation personnel, as described by Cross et al. (1981, 1982); these personnel also collected scale samples from the commercial catches of the Crescent Lake stock (west-side set-net fishery) for comparison to scale samples from the escapement. Utilizing stock-separation techniques and exploitation rates, the total number of returning sockeye salmon was estimated for 1979-1981.

Resident Fish and Recreational Sport Fishery

Available information about the species composition of resident fish and the recreational sport fishery in Crescent Lake is limited to a survey conducted by the ADF&G Sport Fish Division during 20-23 July 1978.

Portable electroshocking equipment, dip net, and minnow traps were used to capture rearing fish in the littoral area of the lake. Electroshocking was conducted for an unknown time period, while four baited minnow traps were deployed for approximately 19 h each. In addition, two variable-mesh gill nets were set for 15 h in the limnetic area to capture resident adult fish. The total number of fish caught and the mean fork length (nearest millimeter) were recorded. Finally, from general observations, most of the recreational sport fishing occurs at the outlet of the lake (in Crescent River). Consequently, field personnel during the 1978 survey were able to interview all fishermen to obtain catch and effort data.

RESULTS

Juvenile Sockeye Size and Age Composition

The fall-period horizontal distribution and relative abundance of juvenile sockeye salmon that were ascertained from net tows at 10 stations (Figure 5) were quite variable. The highest catches occurred near the middle of the lake (Stations 5, 6, and 7), while the lowest catches occurred at each end of the lake (Table 1). The relative abundance (measured as the average number of fish captured for each tow minute, or catch-per-unit effort [CPUE]) for the total catch of sockeye juveniles ranged from zero to 10.05; the mean CPUE was 3.02. The CPUE for age-0.0, age-1.0, and age-2.0 sockeye juveniles were 2.84, 0.15, and 0.01, respectively.

Age-0.0 sockeye salmon juveniles comprised the dominant age class that was caught, accounting for 94.3% of the total catch (Table 2). Age-1.0 juveniles accounted for 5.4%, while the age-2.0 juveniles accounted for less than 1% of the total catch. The average lengths for age-0.0 and age-1.0 juveniles were 43 mm and 57 mm, respectively. The average weights for these juveniles were 0.9 g and 2.1 g, respectively.

<u>1981 Smolt Enumeration, Size, and Age Composition</u>

The estimated number of sockeye salmon smolts migrating from Crescent Lake in 1981, based upon weekly catches and calibrations of capture efficiency of the fyke nets, was 2,011,855 ± 1,270,225 (mean ± 95% confidence interval [Table 3]). In addition to the capture of sockeye salmon smolts, less than 100 each of king salmon, *Oncorhynchus tshawytscha*, smolts, three-spine stickleback, *Gasterosteus aculeatus*, and coastrange sculpins, *Cottus aleuticus*, were also captured by the fyke nets. Nearly 80% of the sockeye smolts captured migrated before the ice had left the lake (19 June), before the water temperature reached 4.0°C, and before maximal river stage height. Peak migration of smolts occurred during the week of 17-23 June.

When there was still ice on the lake (before 19 June), diel sampling indicated that 93% of the sockeye smolts migrated between

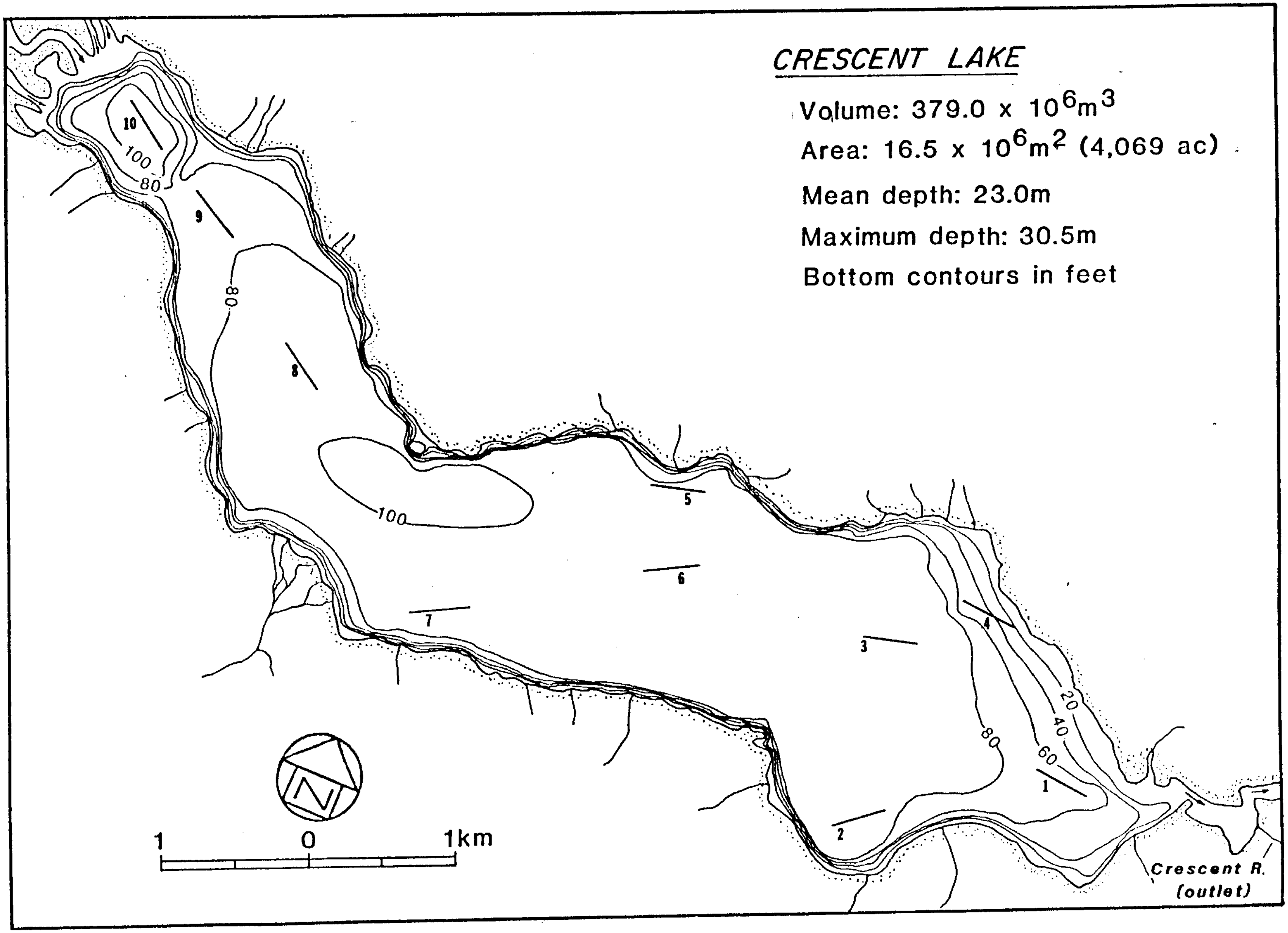

Figure 5. Bathymetric map of Crescent Lake showing townet stations.

Table 1. Relative abundance of juvenile sockeye salmon sampled from Cresent Lake on 25 September 1979.

Date	Tow station	Catch per tow	Catch per tow minute for combined age classes (CPUE)	Mean catch per tow minute (CPUE) by age classes for all stations combined		
				Age 0.0	Age 1.0	Age 2.0
9/25/79	1	15	0.75			
	2	0	0.00			
	3	29	1.45			
	4	8	0.40			
	5	201	10.05			
	6	138	6.90			
	7	152	7.60			
	8	27	1.35			
	9	8	0.40			
	10	25	1.25			
	Mean	60	3.02	2.84	0.15	0.01
	S.D.	73.6	3.68			

Table 2. Mean lengths and weights by age class of juvenile sockeye salmon sampled from Cresent Lake on 25 September 1979.

Age class	Number sampled	Age class composition (%)	Mean sample length (mm)	S.D.	Mean sample weight (g)	S.D.
0.0	282	94.3	43.0	6.0	0.9	0.3
1.0	16	5.4	57.0	4.0	2.1	0.3
2.0	1	0.3	82.0		6.3	

Table 3. Weekly catches and estimates of sockeye salmon smolts migrating from Crescent Lake in 1981.

Weekly period	Mean water temperature (°C)	Weekly catch	Net recapture efficiency	Estimated number of sockeye smolts ± 95% confidence interval
5/20-5/26	1.7	4	--	--
5/27-6/02	2.1	778	--	--
6/03-6/09	2.2	5,855	0.028	246,747 ± 167,962
6/10-6/16	2.6	10,707	0.040	286,198 ± 146,982
6/17-6/23	3.8	5,956	0.007	1,357,968 ± 1,250,412
6/24-6/30	6.6	4,838	0.044	119,045 ± 59,069
7/01-7/07	8.3	313	0.176	1,896 + 927
Total 5/20-7/07		28,451	Estimated Seasonal Total	2,011,855 ± 1,270,225

2000-0200 h. Thus, between 2000-0100 h during 19 May and 19 June, we feel the catch accounted for most of the migrating smolts and, therefore, adequately represented the total migration during this period. After ice-off when the turbidity was much greater because of glacial silt, the diel migratory pattern was inconsistent. For example, 35% of the sockeye smolts migrated between midnight and noon, while 65% migrated between noon and midnight. In addition, half of the sockeye smolts migrated during the brightest part of the day (0600-1800 h) and half during the darkest (1800-0600 h) (Figure 6). Of the eleven days sampled on a 24-h cycle (after 19 June), 6 days were clear and 5 days were overcast and/or raining; however, the diel migratory pattern was virtually the same under both weather conditions (Figure 6). The only diel migratory differences noted follow: 20% of the total smolts migrated during 0600 h to noon on overcast days, compared to 13% of the total on clear days; and 28% of the smolts that migrated during 1800 h to midnight on overcast days increased to 33% on clear days.

Scales, weights, and lengths were taken from 2.1% (589) of the sockeye smolts captured from Cresent River in 1981 (Table 4). Seventy-two percent of these smolts, which averaged 68.1 mm in length and 2.8 g in weight, were age 1.0; whereas, the age-2.0 sockeye smolts averaged 75.6 mm in length and 3.8 g in weight. No age-3.0 sockeye smolts were collected in 1981. Since 67% of the sockeye smolts sampled in 1981 were between 66 and 75 mm long (Figure 7), there was considerable overlapping between the lengths of both age classes. In addition, a moderate decrease in smolt length (10%) and weight (13%) occurred between the first and the last sampling periods (Figure 8).

Considering the weekly age distribution for each 5-mm-size increment, a slight trend toward longer sockeye smolts developed (>71 mm for both age classes); it represented a majority (66%) of the smolts that were caught during the first two sampling periods in

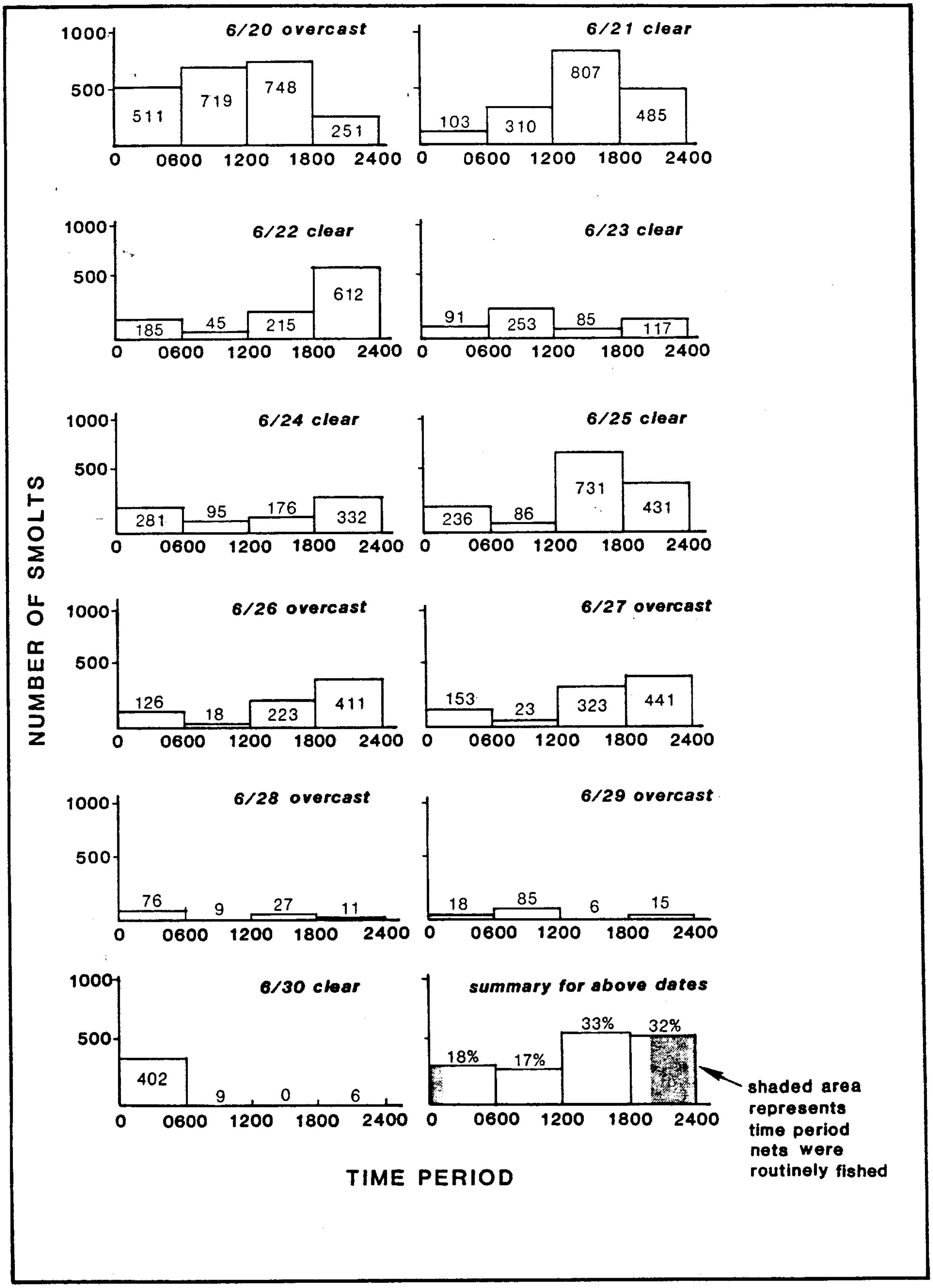

Figure 6. Diel migration pattern of Crescent River sockeye salmon smolts, 1981.

Table 4. Ages, weights, and lengths of sockeye salmon smolts sampled from Crescent River, 1981.

Age class	Number sampled	Age class composition (%)	Mean sample length (mm)	S.D.	Length range (mm)	Mean sample weight (g)	S.D.	Weight range (g)
1.0	424	72.0	68.1	3.9	53.5-79.5	2.8	0.5	1.3-4.8
2.0	165	28.0	75.6	3.0	68.5-86.0	3.8	0.5	2.7-6.1

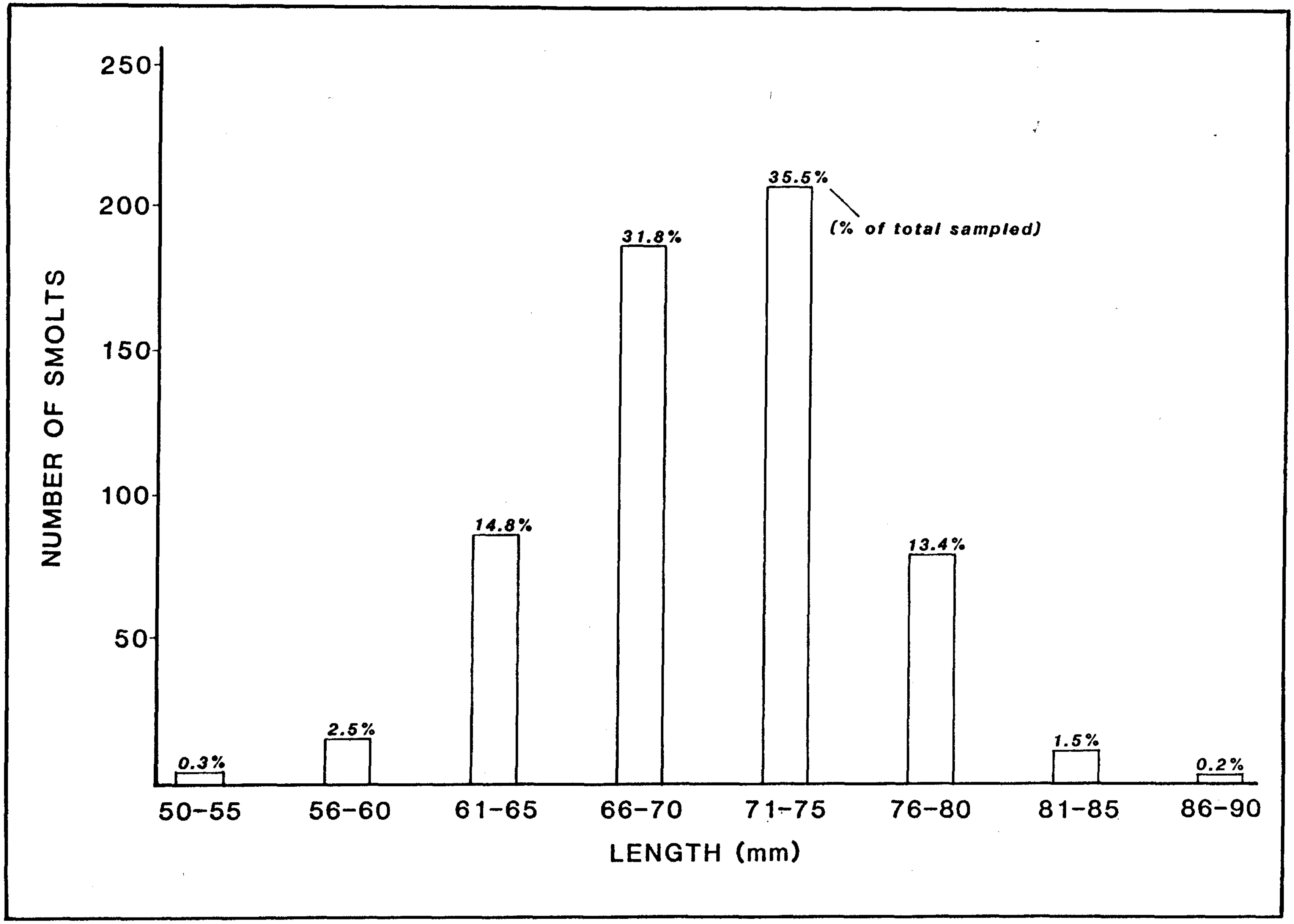

Figure 7. Length frequency distribution of sockeye salmon smolts sampled from Crescent River, 1981.

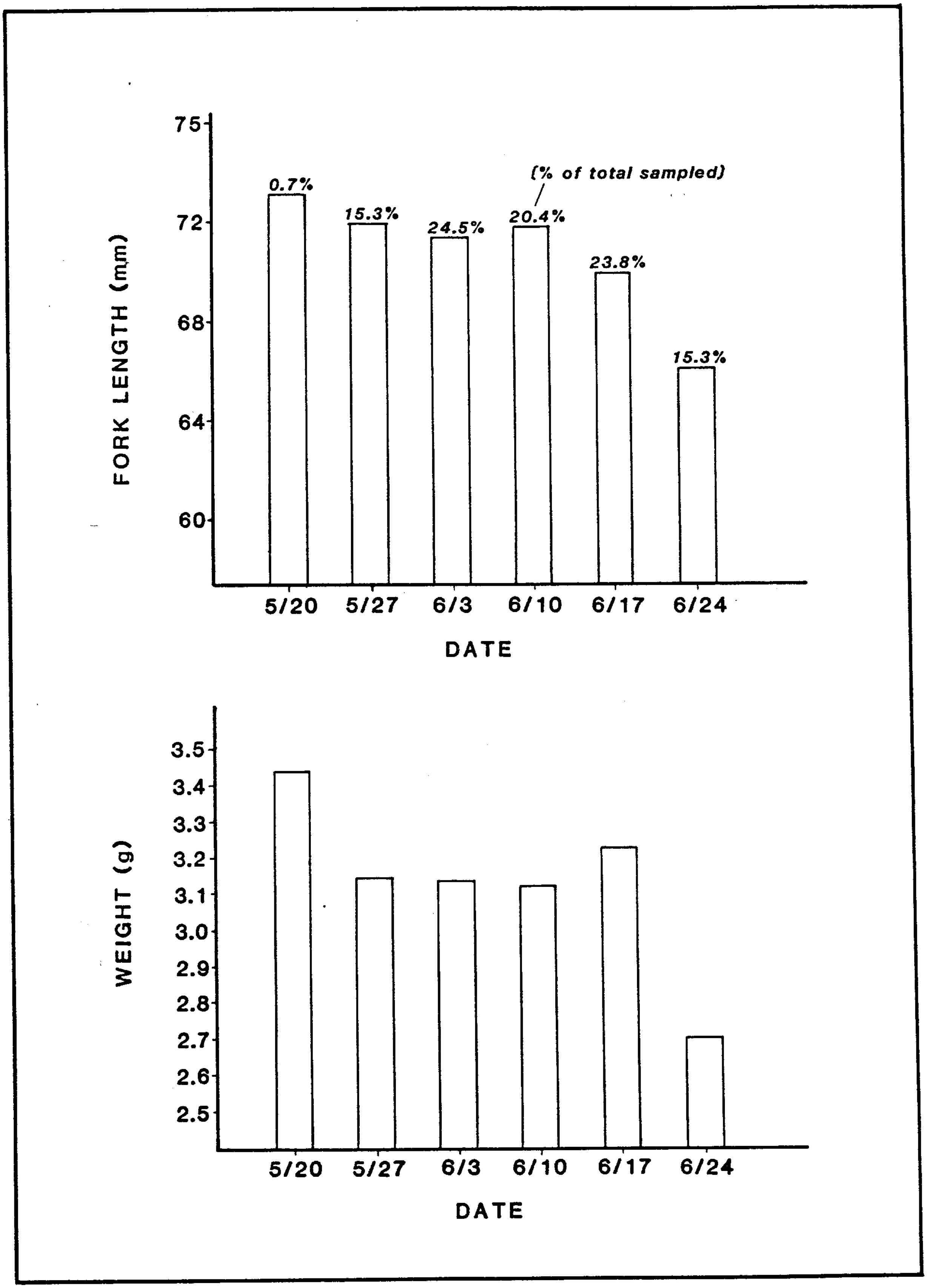

Figure 8. Weekly mean lengths and weights of sockeye salmon smolts sampled from Crescent River, 1981.

May, compared to the last two sampling periods at the end of June when only 33% were >71 mm (Table 5). Similar to the trend in decreasing smolt size was the decreasing occurrence of age-2.0 smolts from early-to-late spring (i.e., from 35% during the first two sampling periods to 22% during the last two) and, hence, an increasing number of age-1.0 smolts from 65% to 78% (Table 5). Thus, two trends were present: a stronger trend of smaller smolts as the spring progressed and a much weaker trend of increased numbers of age-1.0 smolts during the same period. The absence of a significant amount of older smolts migrating earlier could either be a function of sampling bias (i.e., capturing and selecting smaller/younger smolts for measurement) or a naturally occurring characteristic of the migration behavior of sockeye smolts in Crescent Lake during 1981.

<u>1982 Smolt Enumeration, Size and, Age Composition</u>

A conservative estimate of 471,768 ± 79,705 (mean ± 95% confidence limits) sockeye smolts migrated from Crescent Lake in 1982, during 24 May through 6 July (Table 6). The loss of sampling time during the week of 31 May to 6 June (and other brief periods for adjustments of the traps), the escape of marked smolts on 26 June, and general trap avoidance reduced the out-migration estimate by an unknown amount. However, considering the daily catches before and after 31 May to 6 June, the similar migrational timing in 1981, and the estimated trap avoidance, the estimate may have been only 10% to 15% greater.

The peak of migration occurred from 21 to 27 June when the weekly mean water temperature peaked at 6.9° C, soon after the ice had melted off Crescent Lake (Table 6). Nearly 80% of the sockeye smolts captured migrated after ice-out in 1982, compared to 80% of the smolts migrating before ice-out in 1981. In addition, the peak-migration period (21-27 June) occurred when light penetration

Table 5. Weekly age distribution within each 5-mm-size increment of sockeye salmon smolts sampled from Crescent River, 1981.

Length	Age	Week period 5/20-5/26		5/27-6/02		6/03-6/09	6/10-6/16	6/17-6/23		6/24-6/29	Total sampled
51-55	1.0					2					2
	2.0										
56-60	1.0			1		2	1	1		10	15
	2.0										
61-56	1.0			6	32/94=34%	12	7	29	154/230=67%	33	87
	2.0										
66-70	1.0			25		40	39	51		28	183
	2.0					1		1		2	4
71-75	1.0	1		27		48	33	20		6	135
	2.0	2	62/94=66%	9		13	16	24	75/230=33%	10	74
76-80	1.0			1			1	1			3
	2.0	1		19		23	22	10		1	76
81-85	1.0										
	2.0			2		3	1	3			9
86-90	1.0										
	2.0					1					1
Total sampled		4		90		145	120	140		90	589

Table 6. Weekly catches and estimates of sockeye salmon smolts migrating from Crescent Lake in 1982.

Weekly period	Mean water temperature (°C)	Weekly catch	Capture efficiencies	Estimated number of sockeye smolts ± 95% confidence interval
5/17-5/23	4.0	44		
5/24-5/30	4.3	2,886	0.094	32,781 ± 15,886
5/31-6/06[1]	5.1	1,964		
6/07-6/13[2]	4.3	8,282	0.100	85,304 ± 28,167
6/14-6/20	5.6	10,923	0.110	101,286 ± 14,144
6/21-6/27	6.9	17,211	0.094	186,575 ± 49,875
6/28-7/06[3]	6.3	678	0.012	65,822 + 45,135
Total		41,988		471,768 ± 79,705

[1]This period catch is for only 2 days.
[2]By 11 June all ice on the lake had finally melted.
[3]Nine-day period.

in Crescent River began to drastically decrease in depth (Figure 9), and it was similar to the conditions that existed in 1981 (17 to 23 June).

The diel migratory pattern for the peak period in 1982 (21-27 June) showed similarities to the diel pattern observed in 1981, in that the majority (77%) of the captured smolts migrated between 2000 and 0200 h (Figure 10). During the remaining periods (0200-0800 h, 0800-1400 h, and 1400-2000 h), the smolts migrated more uniformally. The only minor exceptions to this migratory pattern were the catches in traps 2 and 4 (Figure 4), in which the majority of smolts migrated between 0200 and 0800 h. However, when combined, these two traps represented less than 3% of the total catch; therefore, the migratory pattern for these two traps is not considered representative. Traps 1 and 5 caught 87% of the total number of smolts captured during the peak-migration period.

Thus, the arrangement of the five traps in Crescent River evidently provided an avoidance/diversion pattern to migrating smolts. That is, the front three traps (traps 2, 3, and 4) must have presented a conspicuous barrier to the migrating smolts, and when avoiding the front traps, they passed into traps 1 and 5. This migration behavior (i.e., the inability of smolts to detect traps 1 and 5) may have been influenced by a velocity shute created between the front traps and by darkness (2000-0200 h) during the time when peak diel migration occurred. In addition, catches from vertical gill nets that were suspended below traps 1 and 5 indicated that 8%-10% of the migrating smolts were migrating below the traps (Table 7). However, this figure must be considered conservative, because when the nets were retrieved, a number of captured smolts were washed out of the nets before being counted.

A subsample of 1,611 sockeye smolts was measured to determine both seasonal mean length and weight. The mean length and weight for all smolts sampled were 71.7 mm and 3.1 g, respectively. The

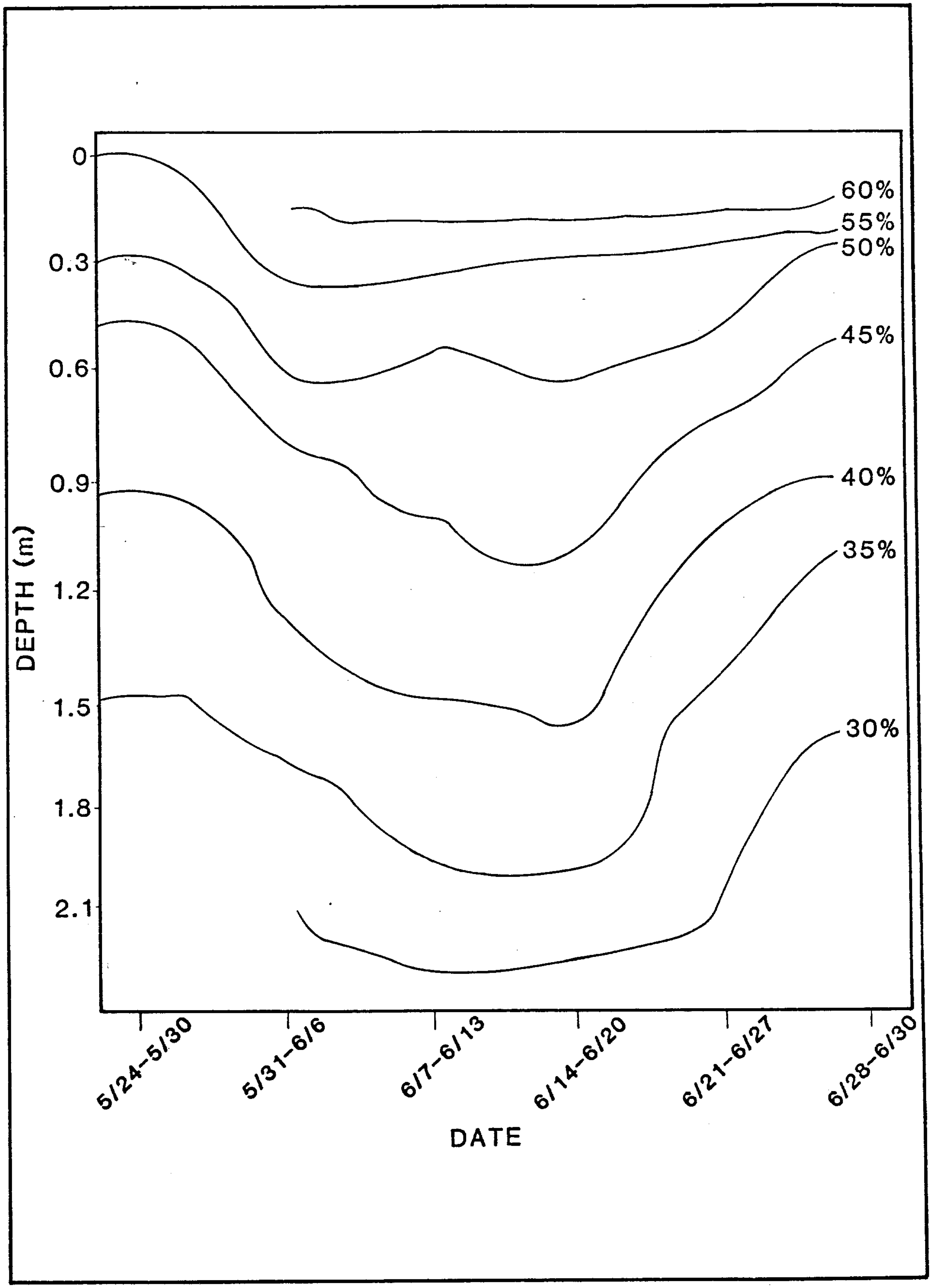

Figure 9. Representative percent incident light isopleths for Crescent River, 1982.

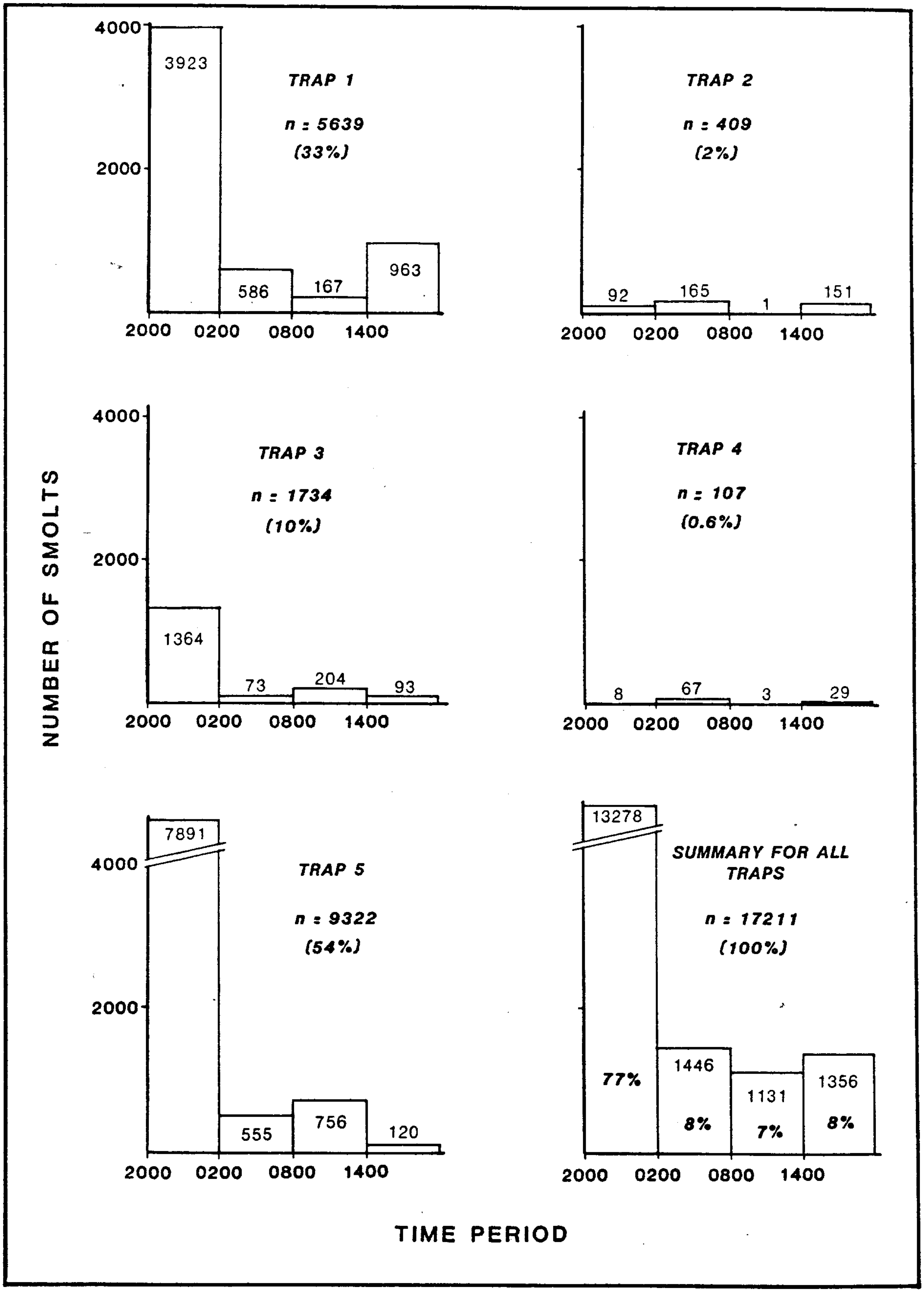

Figure 10. Diel migration pattern for Crescent River sockeye smolts during the week of 21-27 June 1982.

Table 7. Estimated avoidance of traps 1 and 5 by migrating sockeye salmon smolts in Crescent River, 1982.

Date	Number caught in traps		Number caught below traps		Estimated trap avoidance (%)
	Trap 1	Trap 5	Trap 1	Trap 5	
6/15	25	9	2	1	8.8
6/17	52	598	10	42	8.0
6/20	15	106	5	7	9.9

majority (84.1%) of the total sampled was between 66 and 80 mm in length (Figure 11). The age composition was determined from a subsample of 954 sockeye smolts. Age-2.0 smolts dominated the age-class composition, representing nearly 60% of the total (Table 8). The age-1.0 smolts represented 39.6% of the total, while less than 1% were age-3.0 smolts. The mean sizes of the age-1.0 and age-2.0 smolts were 68.7 mm in length and 2.7 g in weight and 75.7 mm in length and 3.6 g in weight, respectively. The weekly mean length gradually increased until the week of 14-20 June; it then continued to slightly decrease until the end of the migration on 5 July (Figure 12). The weekly mean weight showed the same trend as the length, except for the week of 7-13 June when the weight slightly decreased. The weekly age distribution (Table 9) revealed that 85% of the smolts less than 70 mm were age 1.0 and that 83% of the smolts greater than 70 mm were age 2.0. Additionally, in 1982 both the dominance of smolts less than 70 mm and the proportion of age-1.0 smolts decreased with time until after the peak-migration period of 21-27 June when both began to increase.

Adult Enumeration and Sampling 1979-1981

Escapements of 87,000, 91,000, and 41,000 sockeye salmon adults were recorded by the sonar counters for the years 1979-1981, respectively (Table 10). The estimated exploitation rates for the Crescent Lake sockeye stock were based on the stock-separation techniques and the west-side set-net fishery and ranged from 41% to 59%. Thus, the estimated total sockeye adult returns that were based on exploitation rates and sonar-indexed escapements were 210,000 fish in 1979, 154,000 in 1980, and 69,000 in 1981 (Table 10). In addition, the apportioning of other salmon species (based on seine catches at the sonar site in 1979) resulted in the following estimated escapements (Table 11): 3,700 pink salmon, *O. gorbuscha*, 95 chum salmon, *O. keta*, and 122 chinook salmon, *O. tshawytscha*.

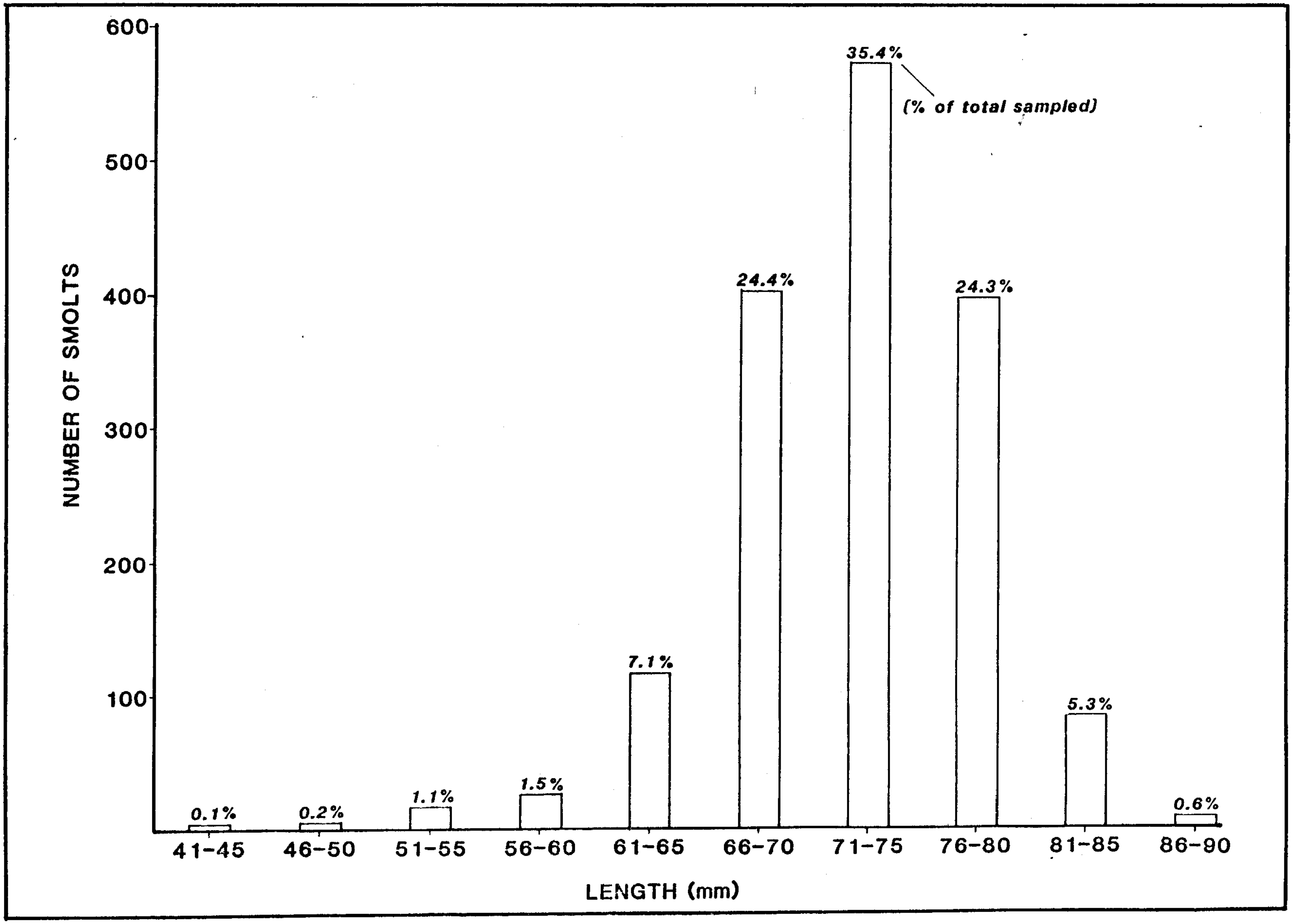

Figure 11. Length frequency distribution of sockeye smolts sampled from Crescent River, 1982.

Table 8. Age, weight, and length data of sockeye salmon smolts sampled from Crescent River, 1982.

Age class	Number sampled	Age class composition (%) ±95% C.I.	Mean sample length (mm) ±95% C.I.	Length range (mm)	Mean sample weight (g) ±95% C.I.	Weight range (g)
1.0	399	39.6 ± 3.5	68.7 ± 0.45	43.5-82.0	2.7 ± 0.06	0.9-4.9
2.0	548	59.6 ± 3.0	75.7 ± 0.34	62.5-88.0	3.6 ± 0.06	2.3-5.8
3.0	7	0.8 ± 0.7	80.2 ± 1.04	76.5-87.0	4.1 ± 0.28	3.6-5.3

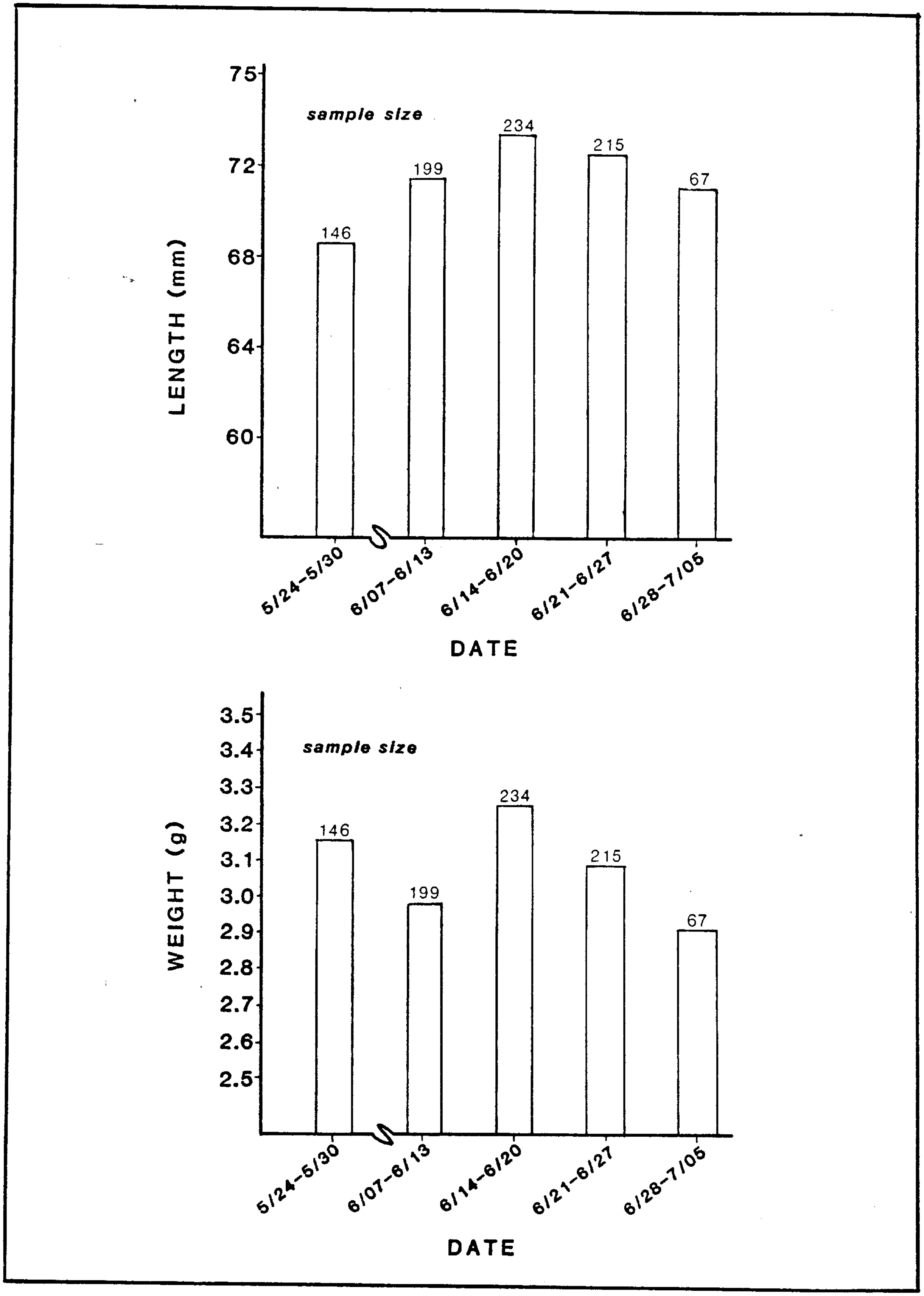

Figure 12. Weekly mean lengths and weights of sockeye smolts sampled from Crescent River, 1982.

Table 9. Weekly age distribution within each 5-mm-length increment for sockeye salmon smolts sampled from Crescent River, 1982.

		Weekly period					
Length	Age	5/24-5/30	6/07-6/13	6/14-6/20	6/21-6/27	6/28-6/05	Total sampled
51-55	1.0	9	1				10
	2.0						
56-60	1.0	9	1				10
	2.0						
61-65	1.0	31	10	5	14	3	63
	2.0				1		1
66-70	1.0	27	29	16	57	38	177
	2.0	6	10	19	14	5	44
71-75	1.0	13	16	15	15	8	67
	2.0	21	44	75	38	8	186
76-80	1.0			2	3	1	6
	2.0	19	36	110	51	7	223
81-85	1.0	1					1
	2.0	3	10	22	10		45
86-90	1.0						
	2.0	2	2	1	3		8
Total sampled		141	159	265	206	70	841
		58%	32%	15%	42%	66%	85% Age 1.0
		64% Age 1.0	36% Age 1.0	14% Age 1.0	43% Age 1.0	71% Age 1.0	83% Age 2.0

Table 10. Summary of escapements, exploitation rates, adult returns, sex and age compositions, lengths, and weights for Crescent Lake sockeye salmon, 1979-1981.

Year	Escapement	Estimated commercial fishery exploitation rate (%)	Estimated adult return
1979	87,000	59.0[1]	210,000
1980	91,000	41.0[1]	154,000
1981	41,000	41.0[2]	69,000

Year	Number sampled	Percent composition by age class[3] 1.1	1.2	1.3	2.2	2.3	Other	Sex composition Female:Male	Mean length range (cm)	Mean weight range (kg)
1979	643	tr	27.8	70.1	tr	tr	tr	1.3:1	48.8-59.0	--
1980	511	--	6.5	86.9	2.9	1.6	2.1	1.5:1	46.6-55.7	1.7-2.9
1981	1,117	--	8.2	32.1	9.6	49.9	tr	1.7:1	47.2-56.6	2.0-3.2

[1]Taken from Cross et al. (1981 and 1982).
[2]Calculated from preliminary catch statistics for west-side set-net fishery.
[3]Percentages weighted for total number in escapement.

Table 11. Daily seine catch by species from Crescent River, 17 July through 9 August 1979.

Date	Daily Seine catch	Sockeye	Pink	Chum	Chinook
7/17/79	31	30	1	0	0
7/18/79	32	30	1	0	1
7/19/79	0[1]	0	0	0	0
7/20/79	0[1]	0	0	0	0
7/21/79	36	32	4	0	0
7/22/79	30	27	3	0	0
7/23/79	0[1]	0	0	0	0
7/24/79	0[1]	0	0	0	0
7/25/79	14	10	4	0	0
7/26/79	24	15	9	0	0
7/27/79	27	15	12	0	0
7/28/79	31	28	2	1	0
7/29/79	27	21	6	0	0
7/30/79	23	22	1	0	0
7/31/79	24	22	2	0	0
8/01/79	22	21	1	0	0
8/02/79	27	25	2	0	0
8/03/79	24	23	1	0	0
8/04/79	17	15	1	1	0
8/05/79	21	20	1	0	0
8/06/79	21	21	0	0	0
8/07/79	0	0	0	0	0
8/08/79	17	16	0	0	1
8/09/79	18	18	0	0	0
Total	466	411	51	2	2

[1]No seining conducted.

Seventy percent of the sockeye adults examined in 1979 and 87% of those examined in 1980 were age 1.3 (Table 10). In 1981 the age composition changed; 50% were age 2.3 and 32% were age 1.3. The mean length for adult sockeye ranged from 46.6 to 59.0 cm during 1979-1981 for all age classes. The dominant age class (1.3) in 1979 and 1980 had mean lengths of 57.8 and 55.7 cm, respectively. In 1981 the dominant age class (2.3) had an average length of 56.6 cm. The average weight ranges for all age classes in 1980 and 1981 were 1.7 to 2.9 kg and 2.0 to 3.2 kg, respectively. No weight data were obtained in 1979. Finally, the mean sex ratio of females to males during 1979-1981 was 1.5 to 1.0.

The migration of sockeye salmon past the sonar counters began during the end of June each year. The peak escapement occurred near 10 July; this indicated a lag time of 10 to 14 days after commercial catches in the west-side set-net fishery began to increase. The mid-point of the sockeye migration was 15 July, while the migration usually terminated in mid-August. In 1979 and 1980, the dominant age class (1.3) entered Crescent River first; it decreased from approximately 80% of the catch in early July to only 50% after 25 July.

A seasonal change in age composition was also apparent in the west-side set-net fishery, in which the catch of age-1.2 fish increased after 9 July (Cross et al. 1981). Thus, earlier entry into the fishery and escapement of 5-year-old fish was characteristic of the Crescent Lake sockeye migration. Finally, stock-separation techniques revealed that the Crescent Lake sockeye accounts for a substantial portion of the catch in the west-side set-net fishery. For example, 64% and 79% of the total catch in this set-net fishery in 1979 and 1980, respectively, were Crescent Lake sockeye salmon (Cross et al. 1981, 1982).

Resident Fish Community

Results of the 1978 survey of fish species residing in Crescent Lake are presented in Table 12. Species caught by electro-shocking were Dolly Varden, *Salvelinus malma*, and coastrange sculpin. The Dolly Varden averaged 61.5 mm in length, while the sculpin averaged 51.0 mm. Gill nets provided the largest catches of fish, including the following: 41 Dolly Varden, 29 lake trout, *S. namaycush*, and 2 juvenile king salmon. The lake trout were the largest-sized species with an average length of 435.7 mm. Twenty sockeye salmon fry and one three-spine stickleback were caught by dip-net near the outlet of Crescent Lake. The sockeye fry averaged 31.8 mm in length and the stickleback was 29.0 mm. No fish were caught by the minnow traps during the 19 h they were fished.

Recreational Sport Fishery

A total of 19 sport fishermen were interviewed during the July 1978 survey. A high catch of 23 fish (primarily Dolly Varden and lake trout) was recorded for 3 anglers during a 20 angler-hour period. Two of the anglers had previously fished at Crescent Lake. Sport Fisheries Division (unpublished data) noted that Crescent Lake receives continuous sport fishing during June through August at a level that may reach 5 anglers/day.

DISCUSSION

The horizontal distribution of juvenile sockeye salmon (based on surface net tows in September 1979) indicated a nonrandom distribution, because the CPUE ranged from 0 to 10 (Table 1). The nonrandom distribution of juvenile sockeye salmon was verified by

Table 12. Summary of resident fish species caught in Crescent Lake during 20-23 July 1978.

Species	Method of capture	Number caught and sampled	Mean length (mm)
Dolly Varden	Electroshocking	4	61.5
Sculpin	Electroshocking	2	51.0
Dolly Varden	Gill net	41	196.8
Lake Trout	Gill net	29	435.7
King salmon	Gill net	2	123.0
Sockeye salmon	Dip net	20	31.8
Stickleback	Dip net	1	29.0

hydroacoustic surveys conducted in September of 1982 (Kyle 1985). However, in the 1982 hydroacoustic survey the majority of fish were found in the inlet half of the lake rather than in the middle of the lake, which was where they were found in 1979, and heavily concentrated in only two areas (Figure 13). In addition, heavy concentrations of fish were found close to the surface during both the day and night surveys conducted in 1982 (Figure 14). Thus, the majority of rearing sockeye juveniles in Crescent Lake were distributed in the middle to upper half of the lake and appeared to occupy surface depths (possibly because of the temperature and/or light penetration dictating areas of successful feeding by sockeye juveniles).

The diel pattern of vertical distribution for juvenile sockeye salmon in Crescent Lake is radically different from that described by Narver (1970) and by Goodlad et al. (1974) for clear-water lakes. Furthermore, a diel pattern similar to that found in Crescent Lake was also observed in the glacially turbid Tustumena Lake (Thomas et al. 1984). The inference from these studies of clear-water and glacially influenced systems is that light regimes that are altered by turbid inflows alter juvenile sockeye behavior relative to that observed in clear-water lakes. The reason for these behavioral changes may be related to the changes in foraging strategy caused by altered zooplankter migration patterns.

Although the age composition of sockeye juveniles in Crescent Lake is similar to that of other Cook Inlet glacial lakes sampled in September, their size is considerably smaller. For example, the Crescent Lake age-0.0 juvenile sockeye in 1979 averaged 43.0 mm in length and 0.9 g in weight (Table 2); whereas, the age-0.0 sockeye juveniles from Skilak, Kenai, and Tustumena Lakes averaged 51.7 mm, 52.4 mm, and 58.8 mm in length and 1.4 g, 1.6 g, and 2.4 g in weight, respectively (Table 13). Thus, smaller-size sockeye juveniles produced in Crescent Lake may indicate inferior rearing

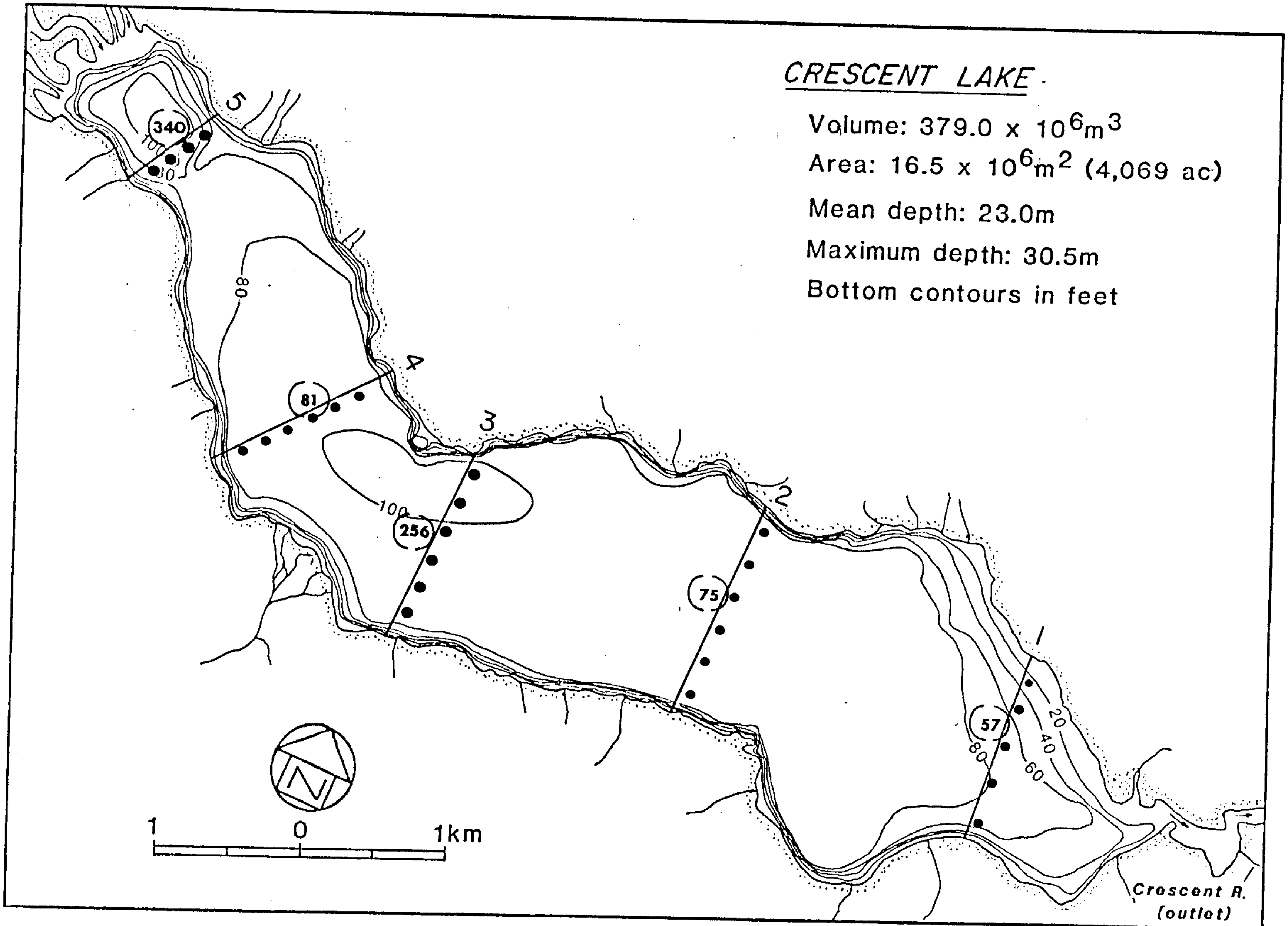

Figure 13. Horizontal distribution of fish densities ($10^3/km^2$) by transects and relative distribution along each transect in Crescent Lake, September 1982.

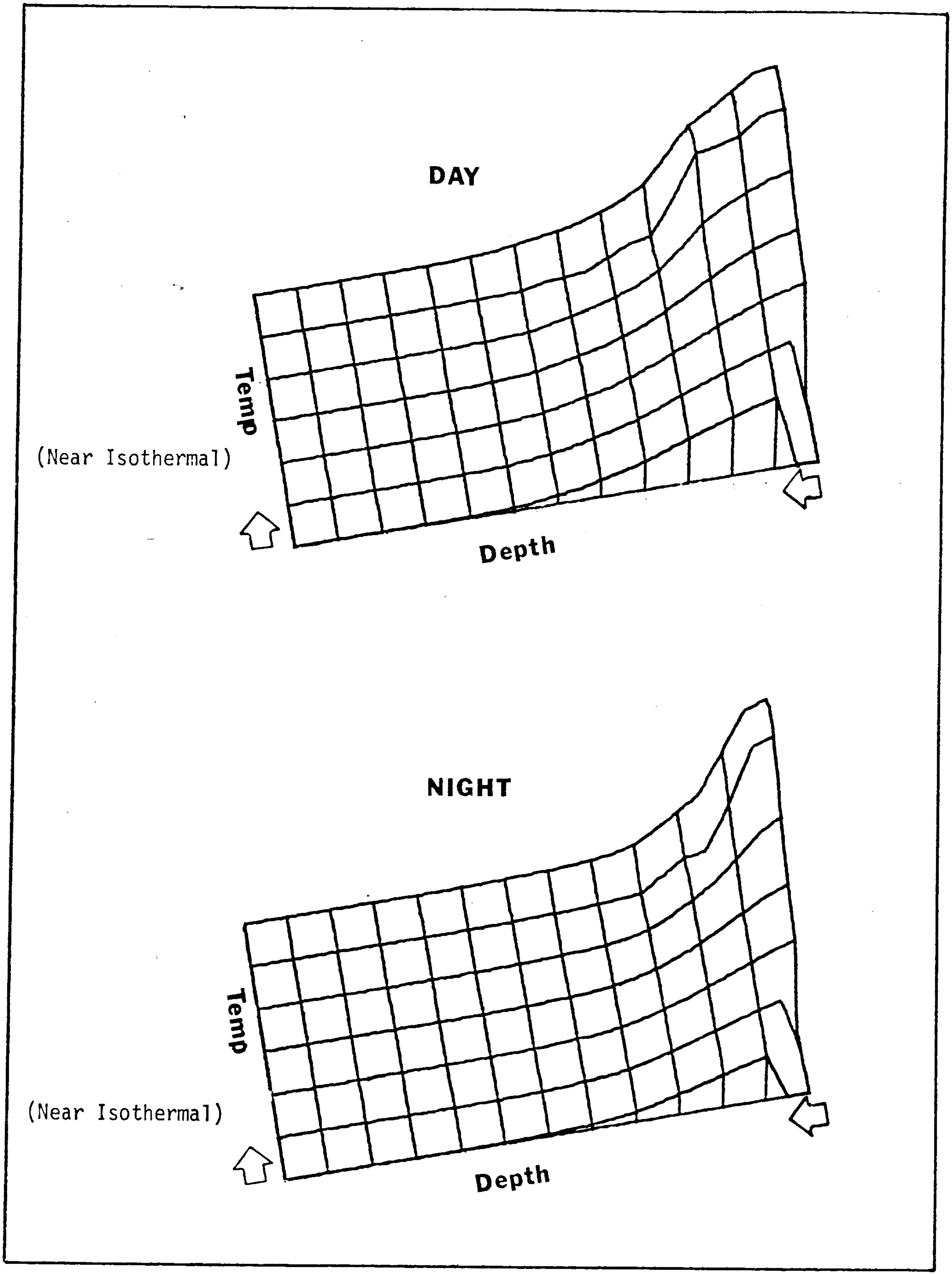

Figure 14. Relative density of fish during day and night surveys in relation to depth and temperature for Crescent Lake, September 1982.

Table 13. Summary of population characteristics of juvenile sockeye salmon sampled from Kenai, Skilak, and Tustumena Lakes during September 1974-1981.

		Age 0.0			Age 1.0		
Year	Date	Percent of catch	Length (mm)	Weight (g)	Percent of catch	Length (mm)	Weight (g)
			Kenai Lake				
1974	09/26	90	60.6	--	10	98.0	--
1975	09/26	94	58.5	2.4	6	80.3	7.5
1976	09/01	97	61.9	2.3	3	81.6	7.3
1977	09/23	99	60.1	2.5	1	77.0	4.8
1978	08/27	100	40.0	0.7	0	--	--
1979	09/05	99	41.1	0.6	1	59.5	2.2
1980	09/19	58	43.2	0.8	42	57.9	2.1
1981	10/14	96	54.1	1.6	4	68.7	3.2
		$\bar{x}$ = 91.6	52.4	1.6	8.4	74.7	4.5
			Skilak Lake				
1974	09/21	92	57.9	--	8	83.3	--
1975	09/24	88	56.3	1.8	12	74.8	4.7
1976	09/01	85	56.0	1.8	15	79.0	5.2
1977	08/21	100	59.0	2.2	0	--	--
1978	08/31	100	43.0	1.0	0	--	--
1979	09/06	99	47.6	0.9	1	76.0	3.8
1980	09/10	88	40.3	0.6	12	53.8	1.6
1981	10/12	89	53.7	1.6	11	62.1	2.8
		$\bar{x}$ = 92.6	51.7	1.4	7.4	71.5	3.6
			Tustumena Lake				
1973	09/23	49	55.8	--	51	75.7	--
1974	09/08	62	61.0	--	38	81.3	--
1975	09/22	86	62.7	2.7	14	86.0	10.0
1976	09/13	97	62.9	3.7	3	84.3	6.6
1977	09/07	96	61.0	2.4	4	83.0	6.2
1978	09/04	95	57.0	2.1	5	81.2	6.2
1979	09/12	97	55.3	1.9	3	81.4	6.3
1980	09/22	92	58.5	2.3	8	79.7	5.7
1981	09/19	91	54.6	1.6	9	73.2	3.8
		$\bar{x}$ = 85.0	58.8	2.4	15.0	80.6	6.4

conditions and accompanying poor survival rates compared to other glacial lakes in Cook Inlet. However, considering sockeye smolt sizes in glacial lakes and in some clear lakes located nearby, the sockeye smolts produced in Crescent Lake were comparable in both length and weight (Table 14).

When compared to other glacial lakes, a possible reason for the small-size juvenile but comparable smolt sizes in Crescent Lake may be the difference in timing of peak zooplankton production. That is, timing of peak zooplankton production in Crescent Lake is known to occur during late August through early September (Part II); whereas, in other Cook Inlet glacial lakes, peaks in zooplankton production occur earlier during mid-June (Koenings 1984). Thus, differences in peak zooplankton production could cause the different juvenile sizes in these glacial lakes.

In 1982 the age composition of sockeye smolts produced in Crescent Lake shifted to a greater number of age-2.0 smolts (60% by composition compared to 30% in 1981). In addition, the observed change in the freshwater-age composition of returning adults in 1982 revealed that smolts produced from Crescent Lake have historically fluctuated in age composition. It is conceivable that previous (but unknown) escapements may partially explain fluctuating smolt ages by invoking cyclic recruitment; however, the varying degree of glacial melt into Crescent Lake, which is dependent upon weather conditions, may be the primary and/or dominant factor causing changes in productivity. That is, increased glacial melt reduces photic-zone depth and epilimnetic temperatures and increases the flushing rate; all of these factors decrease the productive capacity of the lake and delay the seasonal timing of peak zooplankton production. By delaying optimal conditions for primary and secondary production, the peak density of the major forage for rearing sockeye juveniles could be considerably delayed and reduced. Thus, the newly emergent fry may face poor rearing conditions until later in the season (July), when the lake begins to warm and productivity increases.

Table 14. Mean lengths and weights of age-1.0 and age-2.0 sockeye salmon smolts from different systems in Alaska compared to 1981 and 1982 mean lengths and weights of sockeye salmon smolts sampled from Crescent Lake.

Location	Mean length (mm)		Mean weight (g)	
	Age 1.0	Age 2.0	Age 1.0	Age 2.0
	Clear-water lakes			
Hidden Lake	143	200	27.3	83.9
Big Lake	132	166	25.5	48.1
Naknek River	100	113	9.2	12.6
Kvichak River	89	110	6.1	10.1
Togiak Lake	85	101	5.5	9.5
Red Lake	85	111	5.8	12.8
Russian River	84	93	5.1	6.5
Brooks Lake	83	109	5.2	10.1
Desire Lake	74	93	4.7	8.8
Delight Lake	71	81	3.6	5.4
	Glacial lakes			
Tustumena Lake	68	85	2.7	4.8
Crescent Lake (1981)	68	76	2.8	3.8
Crescent Lake (1982)	69	76	2.7	3.6
Kenai Lake	62	72	2.1	3.1

Since freshwater mortality accounts for a large portion of the total mortality that a brood of sockeye juveniles encounters, the most efficient use of natural lakes as a rearing area for sockeye juveniles occurs if the lake is capable of producing age-1.0 smolts. The opportunity to grow quickly to a large size allows for reduced freshwater residency and promotes the production of large yearling smolts. Thus, if sockeye juveniles can maintain a high growth rate and migrate from a lake as high-quality yearling smolts, then survival and productivity during the freshwater life cycle will be enhanced, producing an increase in the number of returning adults.

In respect to Crescent Lake, as with any sockeye-producing lake, the question is one of balancing freshwater and marine survivals when producing large two-year-old smolts versus producing a greater number of smaller one-year-old smolts. In clear-water marine conditions, the size of smolts has been positively related to marine survival (Burgner 1962; Ricker 1962; Barraclough and Robinson 1972). If smolt size relates positively to ocean survival in a marine environment that is turbid (i.e., Cook Inlet) in the same manner that it does in a clear-water environment, then smolt size may be as important as the overall number of smolts. However, given a turbid receiving environment, smolt survival based on size may not be applicable because predation rates are lessened. Thus, the more relevant strategy may become the production of larger numbers of threshold-sized smolts. In Crescent Lake, the aim of a nutrient-enhancement project would be to decrease and stabilize the freshwater residence time (i.e., consistent production of yearling smolts) while, at the same time, producing larger smolts.

In summary, the addition of inorganic nutrients would test the hypothesis that an enhancement and/or alteration of the fertility within this semiglacial lake would provide rearing sockeye juveniles an environment in which survival and growth within the lake would increase. In essence, the enhancement project would allow us to determine if the stock (adult return) would exhibit positive changes in size that reflected the sum of increased freshwater (in a semiglacial system) and marine survival.

Considering Part II of this report, we feel that the addition of nutrients to the epilimnion of Crescent Lake may provide a better rearing environment for sockeye juveniles and, consequently, increase the survival and/or growth rate of the rearing fish by stimulating the production of zooplankters.

If land ownership changes (native acquisition) and/or current land-management policies change so that a nutrient enhancement project could be initiated, further prefertilization studies should be conducted. Specifically, the effect of cool rearing temperatures on growth and/or survival of sockeye juveniles should be evaluated to determine if smolt production is, in part, limited by temperature in Crescent Lake.

ACKNOWLEDGMENTS

I would like to acknowledge the numerous fisheries technicians that conducted the fisheries work, and, in addition, assisted in the trap design and construction of the incline-plane traps used in 1982. Specifically, I would like to dedicate this report in memory of Charley Lamb for his major contributions to the 1982 smolts project. Without Charley's persistence, ingenuity, and willingness to get the job done, the 1982 smolt project would not have been as successful. Finally, I wish to express my appreciation to both Carol Schneiderhan for final drafting all the figures presented in this report, and Sue Howell for typing the manuscripts.

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PART II: Cresent Lake Limnology Program

by

J. P. Koenings
R. D. Burkett

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INTRODUCTION

Many prior studies on the effect of nutrient enrichment on trout and salmon production (Smith 1955; LeBrasseur et al. 1978; Stockner 1981; Frost and Smyly 1952; Munro 1961; Weatherley and Nicholls 1955; Juday and Schloemer 1938; Hasler and Einsele 1948; Nelson 1958, 1959; Tanner 1960; Milbrink and Holmgren 1981a, 1981b) have demonstrated a positive cause-and-effect relationship between increased nutrient supply and fish production. This relationship was recently supported by an empirical model that linked naturally existing total phosphorus concentrations and yield of fish biomass from several lakes (Hanson and Leggett 1982); i.e., as the level of the nutrient-limiting primary production increased from lake to lake, the fish yield increased. In addition, several lake-fertility, fish-production models (e.g. morphoedaphic index) were also tested; the results were significantly less precise, especially when the models were used to compare different types of lakes found over a broad geographic area.

Other studies have sequentially linked increased phosphorus loading to summer primary production (Dillon and Rigler 1974; Vollenweider 1976) and primary production increases to larger fish yields (Nelson 1958; Melack 1976; McConnell et al. 1977). Thus, we feel that a link has been firmly established between nutrient-loading rates and resultant fish production.

It is our intention to evaluate this concept: an increase in biologically available phosphorus in Crescent Lake will stimulate primary production and lead to increased production of sockeye salmon, *Oncorhyncus nerka*, smolt biomass. In addition, we feel that the information that we have already collected should allow the quantitative evaluation of the effect of the nutrient addition within each trophic level. That is, a precisely designed addition of inorganic nutrients that are within the preexisting critical loading rate (Vollenweider 1976) will stimulate primary and secondary production and, consequently, will lead to an increase in sockeye smolt biomass without a detrimental change in water quality.

Description of Study Area

Crescent Lake (60°22'N and 152°65'W) is located on the western side of Cook Inlet (southwest of Kenai) and lies at an elevation of 183 m (Figure 1). The lake has a surface area of 1,647 ha and a maximal depth of approximately 31 m. Because of its typically glaciated U-shaped basin (i.e., small littoral zone and a broad flat bottom), the mean depth (23 m) is only slightly less than the maximal depth (Figure 2). Several inlet streams flow into the lake on an intermittent basis; however, a majority of the inflow comes from overland runoff and from snowmelt originating from more than 3 m of snow pack. Inflow from definable streams consists of meltwater from glacier(s) located on the southwest side of the basin, approximately midway from each end of the lake. The other major tributary is located at the upper end of the lake; however, this stream is considerably clearer, less defined, and more meandering than the glacier-fed, lateral stream systems. Consequently, the major source of cold, turbid runoff originates from the mid-lake lateral streams.

Crescent Lake is the headwater source of the 60-km-long Crescent River, which drains a total watershed (exclusive of the ice fields) of 97,125 ha. The summer discharge of Crescent River is calculated to be 6.2×10^8 m^3 (40 m^3/sec), which results in an ice-free lake-water residence time of 0.6 years, or a flushing rate of once each summer period (June-October). Finally, the estimated annual water residence time was 0.75 yr for 1980 and 0.87 yr for 1981.

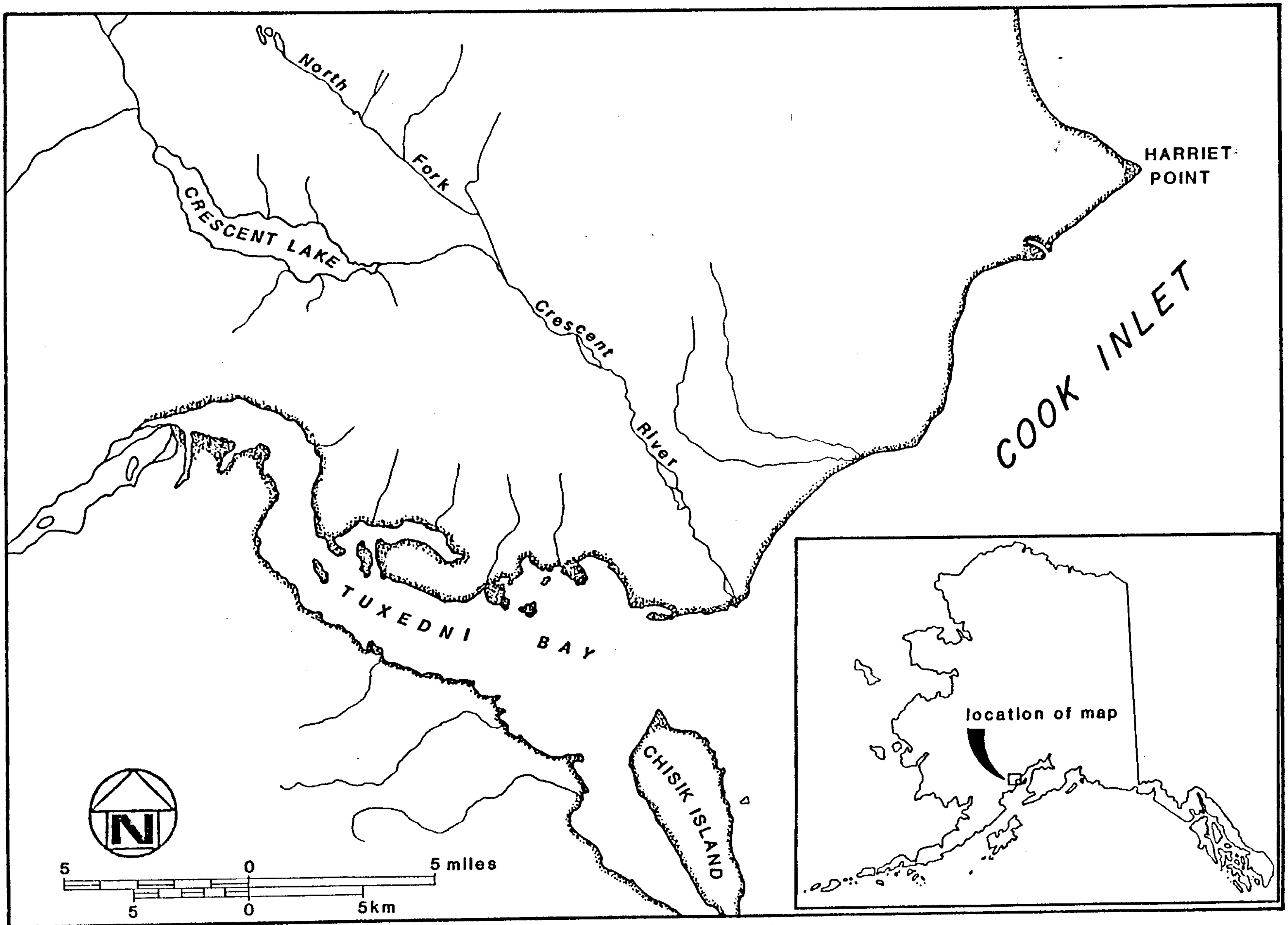

Figure 1. Geographic location of Crescent Lake within the State of Alaska and, specifically, within the Cook Inlet Region of Southcentral Alaska.

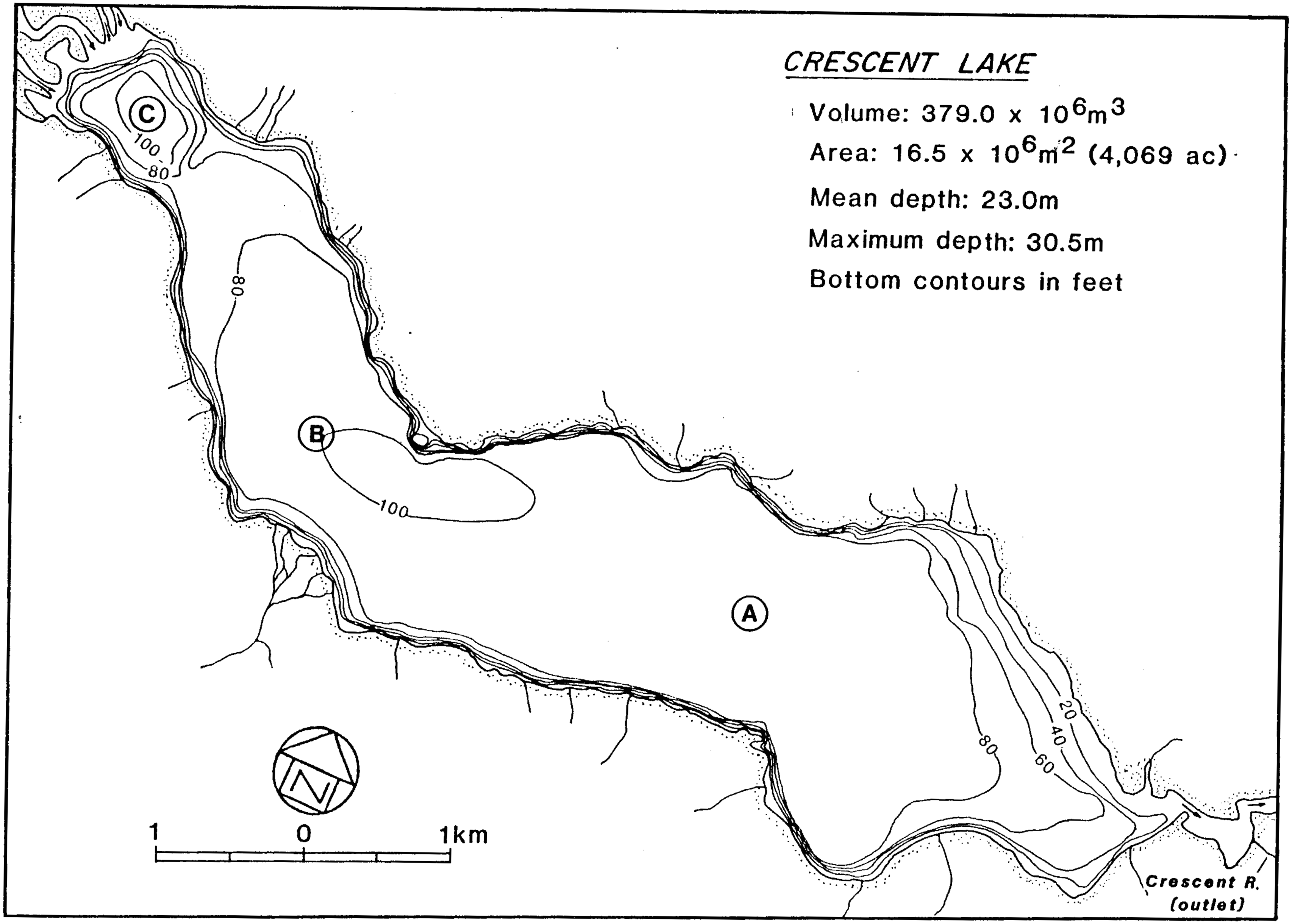

Figure 2. Morphometric map of Crescent Lake showing Stations A and B sampled in 1979-1982, and Station C sampled in 1982.

METHODS AND MATERIALS

Crescent Lake was sampled every three weeks during the period of ice-out (June) to ice-on (November) as well as from one to three times (by plane) during the ice-over period. One station (A) was sampled from July 1979 to the present; a second station (B) was included in the sampling after September 1979, and a third station (C) was added in 1982. The lake was sampled for algal nutrients (nitrogen, phosphorus, silicon, and carbon) as well as for other water-quality parameters (*see* Alaska Department of Fish and Game, Lake Fertilization Guidelines [1979]) from both the epilimnetic (1m) and midhypolimnetic zones. Water samples from multiple (4) casts with a nonmetalic Van Dorn sampler were pooled, stored in 8 to 10 liter transluscent carboys, cooled, and transported in light-proof containers to Soldotna for analysis. Subsequent filtered and unfiltered water samples were either refrigerated or frozen in acid-cleaned, prerinsed polybottles.

All chemical and biological samples were analyzed by methods detailed in Koenings et al. (1985). Filterable reactive phosphorus (FRP) was analyzed by the molybdate-blue/ascorbic-acid method of Murphy and Riley (1962), as modified by Eisenreich et al. (1975). Total phosphorus was determined by the FRP procedure after persulfate digestion. Nitrate and nitrite were determined as nitrite, following Stainton et al. (1977), after cadmium reduction of nitrate. Ammonium analysis followed Stainton et al. (1977), using the phenolhypochlorite methodology, while silicon analysis followed the procedure of Strickland and Parsons (1972). Inorganic carbon was calculated according to Saunders et al. (1962), after determining alkalinity by 0.02 N acid titration to pH 4.5, using a Corning model-399A specific ion meter.

Particulate carbon, nitrogen, and phosphorus were estimated by filtering 1 to 2 liters of lake water through precleaned 4.2-cm GF/F filters. The filters were stored frozen in individual plexislides.

Because of the intermittent level of inorganic glacial silt in Crescent Lake, particulate phosphorus was split into particulate inorganic phosphorus, following the method in Kuenzler et al. (1979). Acidified NH_4F was added to individual filters within a 15-ml centrifuge tube. The tube was shaken for 60 seconds and then filtered. The filtrate was analyzed for reactive phosphorus, and the filter residue for total phosphorus. Particulate inorganic phosphorus was obtained directly from the filtrate analysis, while particulate organic phosphorus was obtained by the difference between the phosphorus remaining on the filter residue and the reactive phosphorus of the filtrate.

Primary production (algal standing crop) was estimated by chlorophyll a (chl a) analysis after the fluorometric procedure of Strickland and Parsons (1972), using the low-strength acid addition recommended by Riemann (1978) to estimate phaeophytin. Samples (1 to 2 liters) were filtered through 4.2-cm Whatman GF/F filters, to which a few milliliters of saturated $MgCO_3$ solution were added just prior to the completion of filtration. The filters were then frozen in plexislides and stored for later analysis.

Primary productivity (rate of photosynthesis) was measured with radioactive carbon (C-14), following the method of Saunders et al. (1962). Samples (two light, one dark, and one dark-killed 100-ml bottles) were placed in situ for 4 hours at 1 m in the mid-euphotic and 1% subsurface light depths during midday (10:00 a.m. to 2:00 p.m.). After incubation, the samples (100-ml bottles) were fixed with 1 ml of Lugols-acetate and filtered under low vacuum (to prevent cellular rupture) on 2.4-cm GF/F glass-fiber filters. The filters were placed in plastic scintillation vials, acidified with 0.2 ml of 1N HCL (Lean and Burnison 1979) to remove residual inorganic carbon-14 from the filters, and assayed after adding 10 ml of Aquasol scintillation fluor on a Packard Tri-carb liquid scintillation spectrometer (*see* Koenings et al. 1985 for detailed methodology).

Zooplankters were collected from duplicate bottom-to-surface vertical tows using a 0.5-m diameter, 153-μm mesh, conical zooplankton net. The net was pulled at a constant 1 m/sec and rinsed well with lake water before removing. Then the organisms were preserved in 10% neturalized sugar-formalin (Haney and Hall 1973). Identification within the genus *Daphnia* followed that of Brooks (1957), while calanoids were identified after Wilson (1959) and copepods after Yeatman (1959). Enumeration consisted of counting triplicate 1-ml subsamples, taken with a Hansen-Stempel pipette, in a 1-ml Sedgewick-Rafter cell. Size (length) of individual zooplankters were obtained by counting at least ten individuals along a transect in each of the 1-ml subsamples used in identification and enumeration. Zooplankters were measured to the nearest 0.01 mm, as described in Edmondson and Winberg (1971). Cyclopoids were split into five size groups:

Nauplii	<0.40 mm
Post-nauplii	≧0.40 mm <0.55 mm
Pre-adult I	≧0.55 mm <0.70 mm
Pre-adult II	≧0.70 mm <0.85 mm
Mature adult	≧0.85 mm

Photosynthetic available radiation (PAR) levels were determined with a Protomatic underwater photometer (Wetzel and Likens 1979), which measures only the 400 to 700 mm wavelengths of light. Water clarity was also measured with a 20-cm Secchi disk by observing the depth at which the disk disappeared from view.

Estimates of yearly phosphorus loading of Crescent Lake were calculated after Vollenweider (1976):

Surface specific loading:

$$Lp\ (\text{mg P/m}^2/\text{yr}) = [P]_c^{sp} \cdot Qs\ (1 + \sqrt{\bar{z}/Qs})$$

Surface critical loading:

$$Lc\ (\text{mg P/m}^2/\text{yr}) = 10 \cdot Qs\ (1 + \sqrt{\bar{z}/Qs})$$

Where: $[P]_C^{sp}$ = spring overturn period total P (mg/m^3)

$Qs = \bar{z}/t_w$

$\bar{z}$ = mean depth (m)

t_w = water resident time (y)

Finally, in both the Tables and Figures we have used the designation of either mg L^{-1} or µg L^{-1} to report concentration data. However, in the body of the report we have used either parts per million (ppm) in lieu of mg L^{-1} and parts per billion (ppb) in lieu of µg L^{-1}. We have made this conversion in order to reduce the handling time of the report by our support staff.

RESULTS

Temperature Isotherms

Crescent Lake was usually covered with approximately 1 to 1.2 m of ice from mid-November to mid-June; the ice-free period lasts 5 months from mid-June to mid-November (Figures 3 and 4). In 1979 isotherms at Station A showed an isothermal state of 4°C in mid-June followed by the rapid warming of the entire water column to 6°C before weak thermal stratification slowly developed above 5 m through the month of July. A seasonal peak temperature of 16°C was observed for a brief period in August; subsequently, the lake rapidly cooled to become isothermal at 7°C in the latter part of September. In 1980 temperatures were again at 4°C soon after ice-out; however, warming was less intense, with thermal stability lacking for most of the year. In 1980 maximal temperatures of only 10°C were reached in July and August. In August wind-generated mixing warmed the lake as surficial isotherms were pushed deep into the lake. Following this, the lake rapidly cooled, reaching an isothermal 5°C condition by October. In contrast to thermal conditions in 1980, the lake was isothermal for only a very short

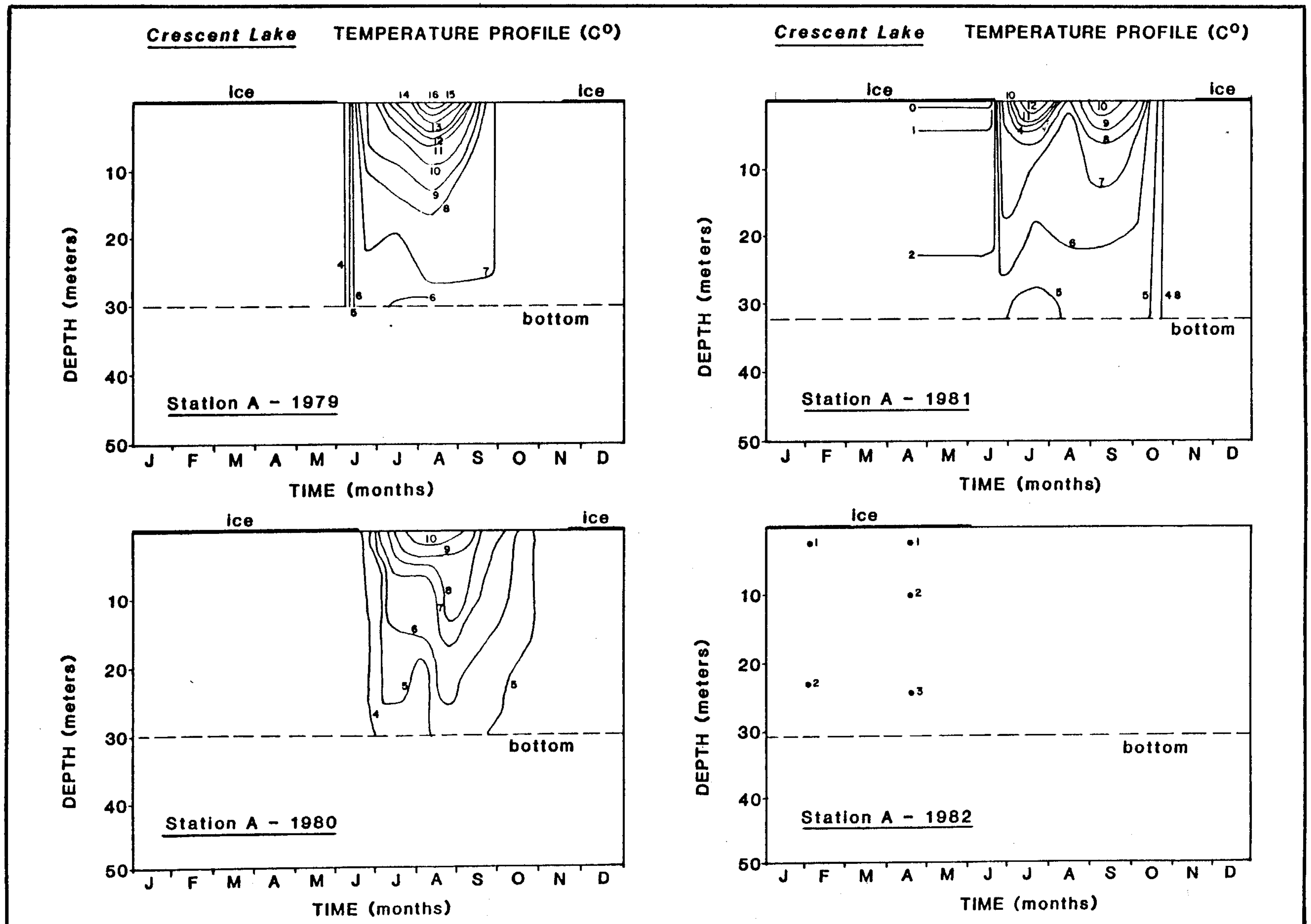

Figure 3. Temperature isotherms (°C) for Station A in 1979, 1980, and 1981.

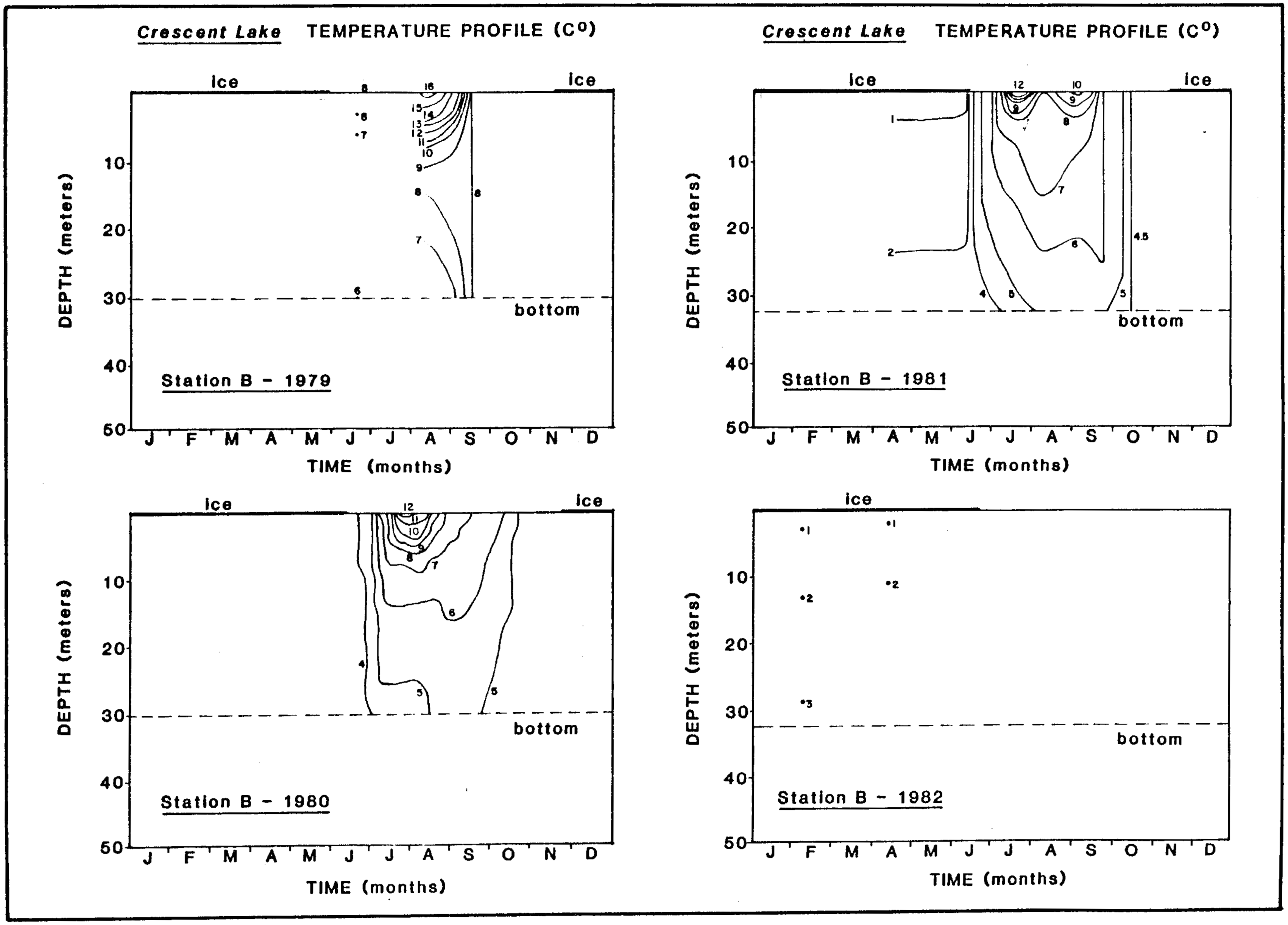

Figure 4. Temperature isotherms (°C) for Station B in 1979, 1980, and 1981.

time in the spring of 1981 before a strong thermal structure developed in July at ≅4 m. Maximal temperatures of >12°C were recorded for this period; however, shortly thereafter, the lake cooled dramatically, with almost a complete loss of thermal structure. Following this cooling period, the lake warmed to only 10°C before cooling again to an isothermal condition of 5°C by October.

Although the general trends in thermal structure at Station A were repeated at Station B, significant differences were noted. For example, in 1980 the thermocline at Station B not only developed earlier than at Station A, but it developed much more strongly. In addition, maximal temperatures exceeded 12°C at Station B compared to 10°C at Station A, and the subsequent cooling at Station B, was significantly slower than that found at Station A.

In 1981 the rate of warming at Station B was slower in the early spring period, but temperatures generally equalled those at Station A. In addition, the cooling of the lake in August was still in evidence at Station B, but the degree of heat loss was less severe (i.e., the 6°- 7° C isotherms remained low in the water column); whereas, at Station A they rose almost to the surface. Finally, temperatures under the ice during the winter period remained at 4°C at both stations; however, temperatures reported for April of 1981 and those for April of 1982 were slightly but consistently higher at Station B, compared to those at Station A. This suggests that Station A and B were located within different water masses and subjected to different thermal influences.

Light-Penetration Isopleths

The penetration of photosynthetically available radiation (PAR) varied considerably within a season and between stations (Figures 5 and 6). In 1979, soon after ice-out in early spring, light

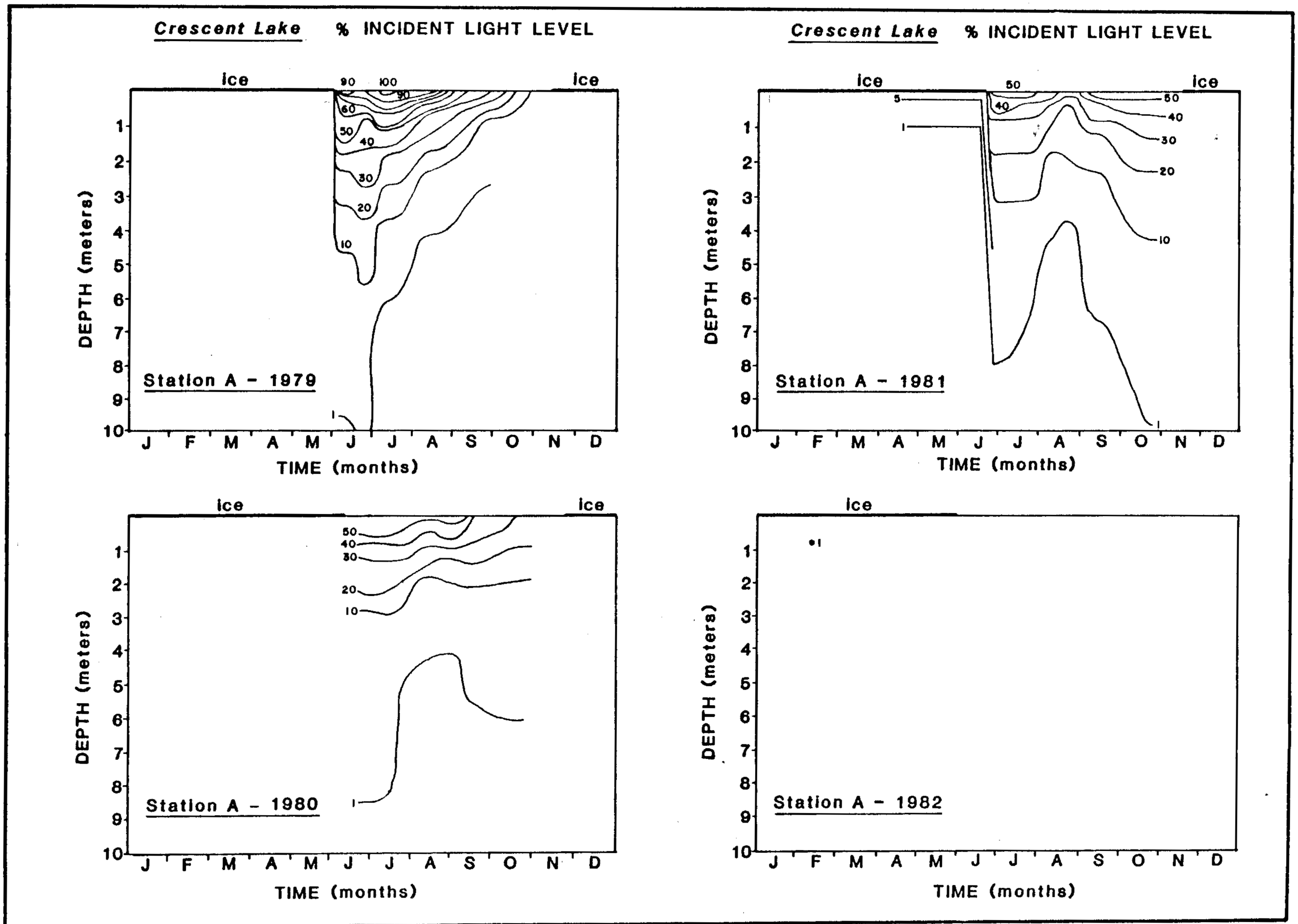

Figure 5. Photosynthetically available radiation (PAR) isopleths by depth for Station A in 1979, 1980, and 1981.

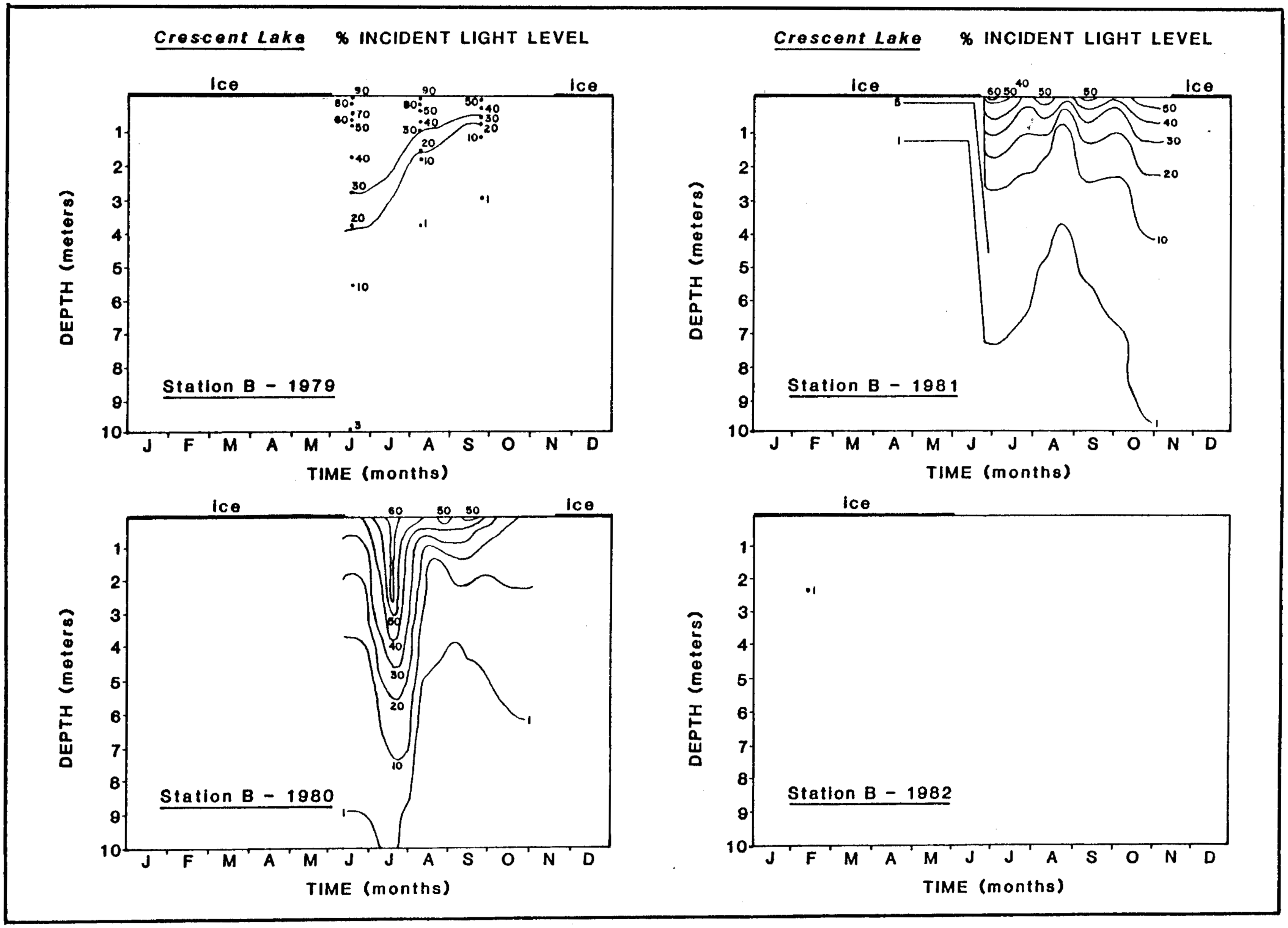

Figure 6. Photosynthetically available radiation (PAR) isopleths by depth for Station B in 1979, 1980, and 1981.

penetrated from 10 to 11 m at Station A. At the end of June, light penetration receded so that by the end of September the euphotic zone (defined as the deepest penetration of 1% sub-surface light) was reduced to only 3 m. In 1980 the oscillations of the light isopleths were considerably dampened, showing a distinct change from 1979. Instead of the light-compensation depth decreasing with time from July through October as in 1979, light penetration actually increased between August and October. The depth of the euphotic zone varied from ≅9 m in the spring to ≅4 m in August and then increased to ≅6 m by the end of October. This pattern was amplified in 1981 because the euphotic zone extended to 8 m in June, then decreased dramatically to 4 m in August, and again increased to ≅10 m by late October.

Although light penetration at Station B followed the same general seasonal pattern as at Station A, important differences were noted. In 1980 light penetration at Station B was dramatically deeper in June and July, but from August on it followed the same trend noted at Station A; i.e., a reduction in the euphotic zone depth until August (approximately 4 m) followed by an increase to a depth of approximately 10 m by October. Again in 1981, light-penetration isopleths at Station B followed the same overall trend as Station A, but Station B showed isolated pockets of surface clearing. That is, the depth of the euphotic zone extended to approximately 8 m in the spring, decreased to 4 m in August, and finally deepened to approximately 10 m in October. The light-penetration profiles support the concept that somewhat discreet water masses, under separate environmental influences, are present at Stations A and B during portions of the ice-free season.

Dissolved Gases

Dissolved oxygen was consistently greater than 90% of saturation during all dates and at all depths sampled. Increases or decreases in oxygen concentration were not biologically mediated; instead, these variations merely reflected a decrease or increase in temperature.

General Water-Quality Parameters

Although general water-quality parameters (Table 1) varied little in Crescent Lake, there was a consistent trend for lower alkalinity and conductivity levels during August and September, compared to the rest of the year. The degree of within-season variation appeared to be dependent on the magnitude of glacial meltwater intrusion. That is, in 1980 when glacial input was not as extensive as in 1981, alkalinity levels remained virtually constant (≅10 ppm), and conductivity values dropped from ≅35 μmhos cm^{-1} to ≅25 μmhos cm^{-1}. However, in 1981 when glacial meltwater (or the ratio of glacial meltwater to clear-water runoff) was greater, alkalinity values dropped from ≅14 ppm to ≅7 ppm, and conductivity levels decreased from ≅35 μmhos cm^{-1} to ≅15 μmhos cm^{-1}. However, this trend did not extend to metals because calcium levels remained constant (4-5 ppm), as did magnesium; i.e., undetectable. Iron concentrations rose from 100 ppb in the spring (June) to peak levels of >350 ppb during the August-September period and then dropped in late October to ≅100 ppb.

Inorganic Nutrient Cycles

Inorganic nitrogen concentrations (nitrate + nitrite) showed distinct seasonal patterns within both the epilimnion and the hypolimnion (Figure 7). In general, the amount of nitrate + nitrite throughout a year was consistently high (≧150 ppb); high-cycle concentrations occurred in early spring (June through July; i.e.,) at over 350 ppb in 1980 and >300 ppb in 1981. Lower concentrations were observed from August to the beginning of November; i.e., dropping to minimal levels of ≅225 ppb in 1980 and ≅150 ppb in 1981. Nitrate levels then increased in both years throughout the ice-over period, peaking just after ice-off in the spring.

Differences in nitrate concentration between stations were slight; however, small differences did arise between the hypolimnetic and

Table 1. General water-quality parameters at Stations A and B (combined) for the epilimnion taken during 1980 and 1981.

Parameter	Seasonal Mean Values ± S.D. 1980	1981
Conductivity (µmhos cm^{-1}) @ 25°C	28 ± 4.5 (n=28)	22 ± 8.2 (n=28)
pH*	6.80 (n=28)	6.17 (n=28)
Total Dissolved Solids (mg L^{-1})	23 ± 5.6 (n=28)	Not available
Alkalinity (mg L^{-1} as $CaCO_3$)	10 ± 1.6 (n=28)	10 ± 2.7 (n=28)
Calcium (mg L^{-1})	4 ± 0.7 (n=28)	5 ± 0.8 (n=28)
Magnesium (mg L^{-1})	<0.5 (n=28)	<0.5 (n=28)
Iron (µg L^{-1})	218 ± 144 (n=24)	186 ± 108 (n=19)

*Calculated from mean anti-logs.

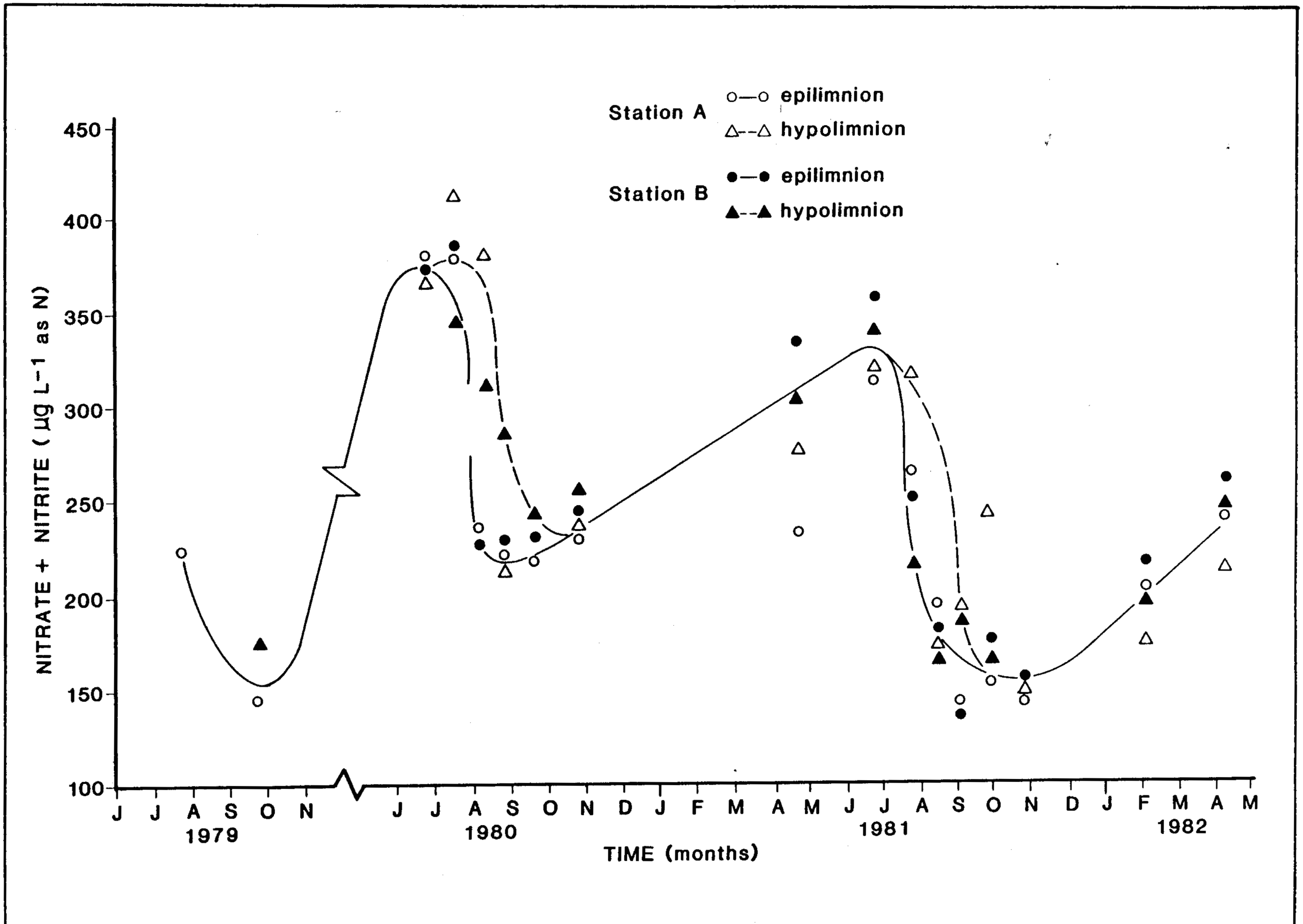

Figure 7. Seasonal cycle of inorganic nitrogen (nitrate + nitrite) in the epilimnion and hypolimnion of Crescent Lake in 1979, 1980, and 1981.

epilimnetic strata. These differences became apparent during the summer period (July through the beginning of September) and were presumably due to biological uptake of nitrate. However, large-scale variations in the introduction of snowmelt, precipitation, and glacial input combined to produce the larger part of the seasonal oscillation found for nitrate levels.

Ammonium levels within the lake varied seasonally, falling below detectable values (<0.5 ppb) in July through September of 1980 and at the end of June 1981. Ammonium levels increased at the end of fall (October), preceeding the increase in nitrate in both 1980 and 1981. However, levels of ammonium were consistently low (usually falling below 20 ppb) and showed a great variability between sampling dates, depths, and stations. Thus, substantial and consistent differences between the epilimnion and hypolimnion were not apparent.

Silicon Profiles

Levels of reactive silicon were consistently high, reaching nearly 3,000 ppb in the spring of 1980 and ≅2,500 ppb in the spring of 1981 (Figure 8). Seasonally low levels were reached in late August 1980 (2,200 ppb) and in late September 1981 (1,800 ppb). Like the nitrate profiles, both stations contained equivalent concentrations of reactive silicon; however, compared to the hypolimnion, lower levels of silicon within the epilimnion became apparent only during the July-August period of 1980.

Phosphorus Profiles

Epilimnetic total phosphorus (TP) concentrations in 1980 oscillated from a low of 3.5 ppb in the spring (June) to a peak of slightly greater than 10 ppb in early September before receding back to 3.5 ppb by late fall (Figure 9). This general seasonal pattern repeated itself in 1981: TP moved upward from ≅4 ppb in April, peaked at 9.5 ppb by August, and then fell to ≅4.5 ppb in the fall

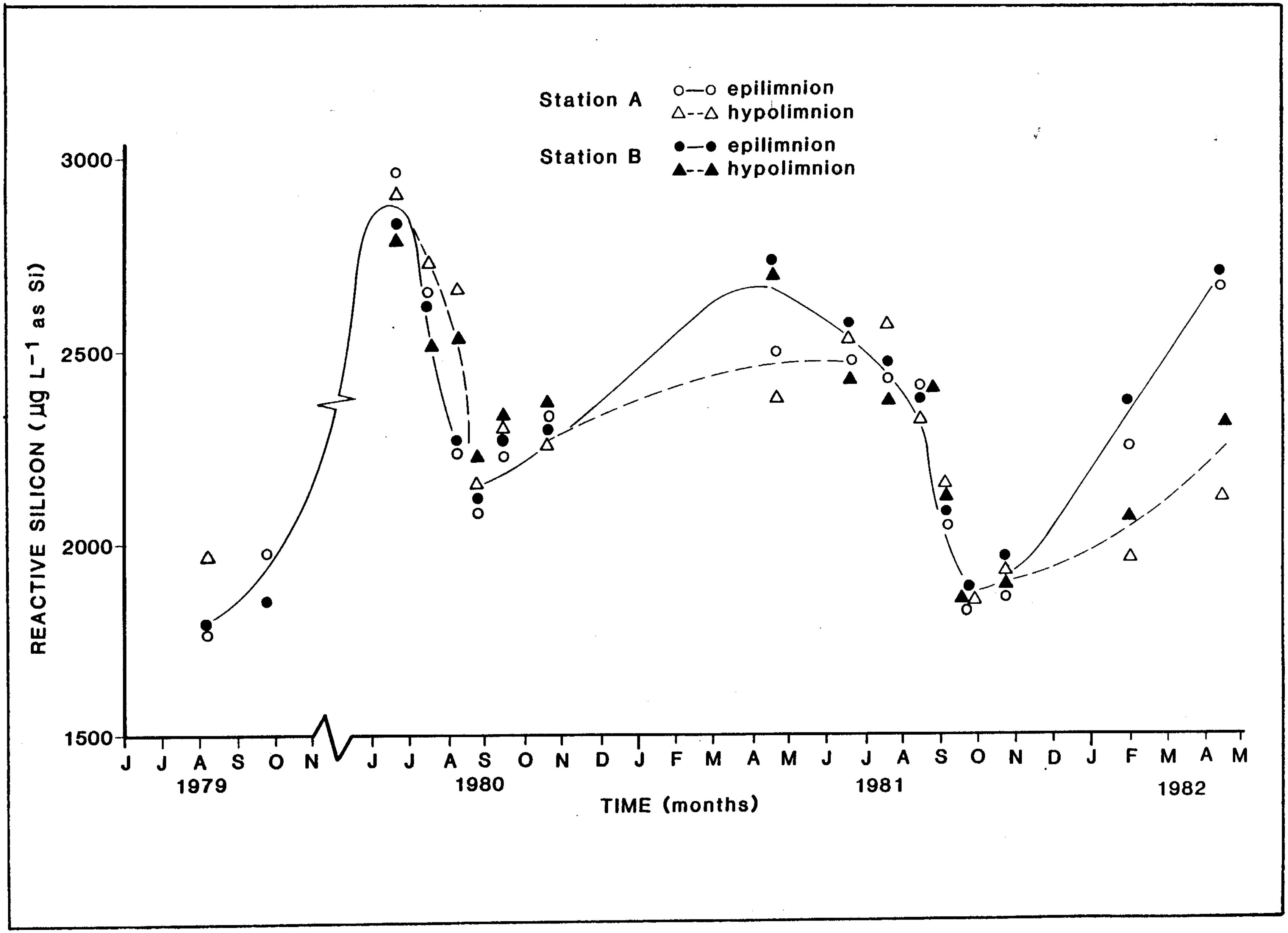

Figure 8. Seasonal profiles for reactive silicon in the epilimnion and hypolimnion of Crescent Lake in 1979, 1980, and 1981.

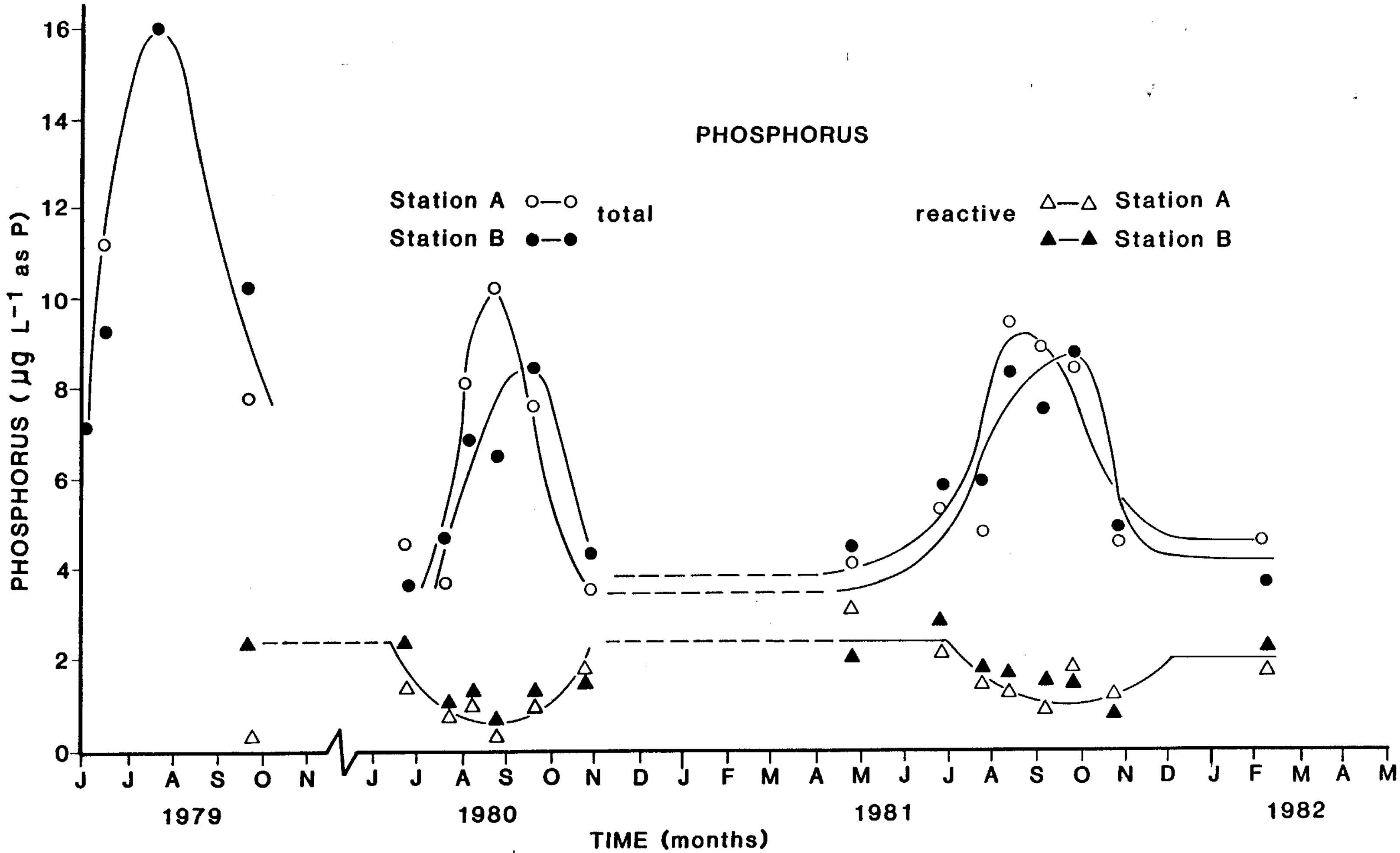

Figure 9. Seasonal profiles of total and reactive phosphorus in the epilimnion of Crescent Lake in 1979, 1980, and 1981.

(October). This pattern also repeated itself at both stations; the slightly higher peak values at Station A preceeded those at Station B in both 1980 and 1981. Yearly mean concentrations of TP equalled 7.0 ppb and 7.3 ppb in 1980 and 1981, respectively.

Reactive phosphorus (RP) concentrations showed a seasonal cycle that was much different than that of total phosphorus. Minimal values (≅1.0 ppb of RP) were found in August and September; slightly higher values (>2.0 ppb) were present in both June and October of 1980 and 1981 (Figure 9). In general, reactive phosphorus levels were near the level of detectability throughout the lake soon after ice-out in the spring and reached their highest concentrations under the ice in April of 1981 and in February-April of 1982. Yearly mean concentrations of reactive phosphorus equalled 1.2 ppb and 1.8 ppb in 1980 and 1981, respectively.

Particulate Phosphorus

In 1979, 1980, and 1981, particulate phosphorus represented over 75% of the total phosphorus found in Crescent Lake. In clear-water lakes, a majority of particulate phosphorus is considered to be organically bound phosphorus held primarily within the cells of phytoplankton, bacteria, and detritus. As such, it becomes available to the pool of metabolically active phosphorus that continually recycles through the plankton. However, in glacially influenced lakes, inorganic silt clouds the water for most of the ice-free season. The following question arose: was a majority of the particulate phosphorus bound within the inorganic glacial flour rather than being held within the organic seston? If so, this fraction would not consist of biologically available phosphorus (BAP) and should be subtracted from loading calculations formed from clear-water lakes, within which the particulate inorganic phosphorus fraction is insignificant.

Over 65% of the particulate phosphorus within the epilimnion proved to be inorganic particulate-P (Figure 10). This fraction

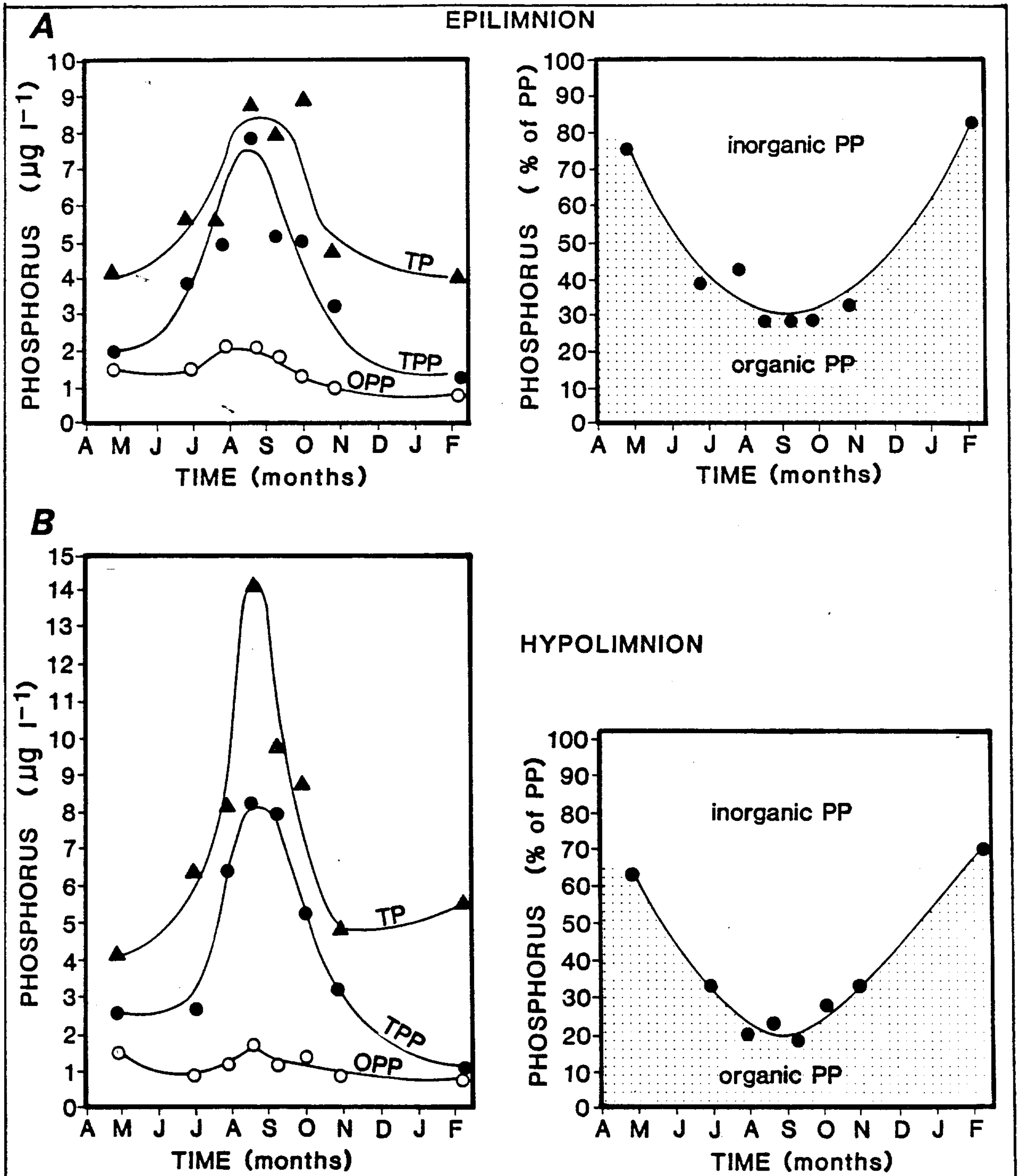

Figure 10. Seasonal cycles of total phosphorus (TP), total particulate phosphorus (TPP), and organic particulate phosphorus (OPP) in the epilimnion (A) and hypolimnion (B) of Crescent Lake, 1981.

increased to over 75% in the hypolimnion (Figure 10); i.e., only 35% of particulate-P in the epilmnion and 25% of particulate-P in the hypolimnion are bound in an organic faction. Correcting for this inorganic phosphorus would reduce the total phosphorus concentration considered to be biologically active by nearly 50%. In addition, the contribution of inorganic particulate-P was not consistent over time: varying from only 20% of particulate-P under the ice in April of 1981 and February of 1982 (when the lake was substantially clear) to over 70% during the summer period of August and September (Figure 10).

Finally, the difference between particulate-P and total-P was much greater in the hypolimnion, compared to the same time periods within the epilimnion. For example, on 13 August non-particulate-P equalled <1 ppb in the epilimnion but was over 6 ppb in the hypolimnion. This suggests that within the euphotic zone non-particulate-P was being converted to a larger extent to particulate-P. However, total particulate-P in both strata was approximately 8 ppb, so the difference was due to a larger fraction of non-particulate-P entering the hypolimnion (perhaps from the sediments). Finally, comparable levels of total particulate-P in both the epilimnion and the hypolimnion suggest a lack of glacial silt sedimentation throughout the year in Crescent Lake.

Phytoplankton Standing Crop and Carbon Uptake Rates

The standing crop of phytoplankton showed a fairly distinct seasonal pattern in Crescent Lake; peak chl *a* concentrations occurred in August (1979) and in early September (1980 and 1981) (Table 2). Peak chl *a* values ranged from 1.93 mg/m^3, 1.96 mg/m^3, and 1.71 mg/m^3 at Station B to 2.05 mg/m^3, 5.20 mg/^{3}, and 1.97 mg/m^3 at Station A during 1979, 1980, and 1981, respectively. Considering both stations, the highest concentration of chl *a* was found in 1980 and the lowest in 1981. Whereas the chl *a* levels at both stations followed a similar seasonal pattern, Station A contained a slightly greater quantity of chl *a*, both in terms of

Table 2. Chlorophyll a (mg/m^3) levels found within the epilimnion and hypolimnion of Crescent Lake in 1979, 1980, and 1981.

	Station A		Station B	
Date	Epilimnion	Hypolimnion	Epilimnion	Hypolimnion
07/17/79	1.06	0.19	--	--
08/05/79	2.05	0.16	1.93	0.42
09/25/79	0.15	0.35	0.34	0.59
06/25/80	0.48	0.39	0.82	0.53
07/16/80	0.23	<0.10	0.35	0.06
08/07/80	0.50	0.15	0.70	0.06
08/26/80	0.50	0.28	0.42	0.14
09/17/80	5.20	0.70	1.96	0.30
10/29/80	0.55	0.29	0.41	0.29
04/20/81	1.18	0.13	0.27	0.02
06/30/81	0.46	0.46	0.05	0.13
07/21/81	0.25	0.10	0.46	0.04
08/13/81	0.25	--	0.24	0.30
09/04/81	1.97	0.39	1.71	0.39
09/30/81	0.59	0.59	0.15	0.39
10/22/81	0.31	0.33	0.16	0.39

peak concentration and of summer seasonal averages. Epilimnetic chl _a_ for the June through October period averaged 1.24 mg/m^3 (n=6) and 0.64 mg/m^3 (n=6) at Station A and 0.78 mg/m^3 (n=6) and 0.45 mg/m^3 (n=6) at Station B in 1980 and 1981, respectively.

Hypolimnetic (<30 m) chl _a_ levels were consistently lower and less variable than those in the epilimnion. Mean concentrations for the June through October period were 0.35 mg/m^3 (n=6) and 0.37 mg/m^3 (n=6) at Station A and 0.24 mg/m^3 (n=6) and 0.27 mg/m^3 (n=6) at Station B in 1980 and 1981, respectively. However, unlike the epilimnion, a peak in chl _a_ during the later part of August and early September never developed. Peak levels of chl _a_ within the hypolimnion occurred in the spring and fall as a consequence of mixing with the epilimnetic layer during the lake-overturn periods.

Unlike chl _a_ concentrations, which are less susceptible to short-term variability within a definable water body, photosynthesis is dependent on day-to-day variations in light, temperature, and nutrient supply. In addition, the number (biomass) of algal cells as well as general nutritional status are also important. Consequently, the magnitude and shape of the photosynthetic depth curve varied considerably by sampling period and by sampling station (Figure 11). By locating our in-situ incubations within the ever-changing photic zone, we observed that as the photic zone shallowed (in response to the turbidity imparted by glacial meltwater intrusion), volumetric carbon uptake rates tended to change. Using events in 1981 as an example, daily volumetric uptake rates ranged from 7 mg C/m^3 to 77 mg C/m^3 prior to meltwater input; this compares to rates of 2 mg C/m^3 to 3 mg C/m^3 at the height of the intrusion (13 August). Later in the year as the lake cleared, the uptake rates increased to 15 mg C/m^3 - 21 mg C/m^3 but then decreased by late October to 4 mg C/m^3 to 5 mg C/m^3. However, as the volumetric rates decreased, so did the areal estimates, because the photic zone decreased in depth from 8 to

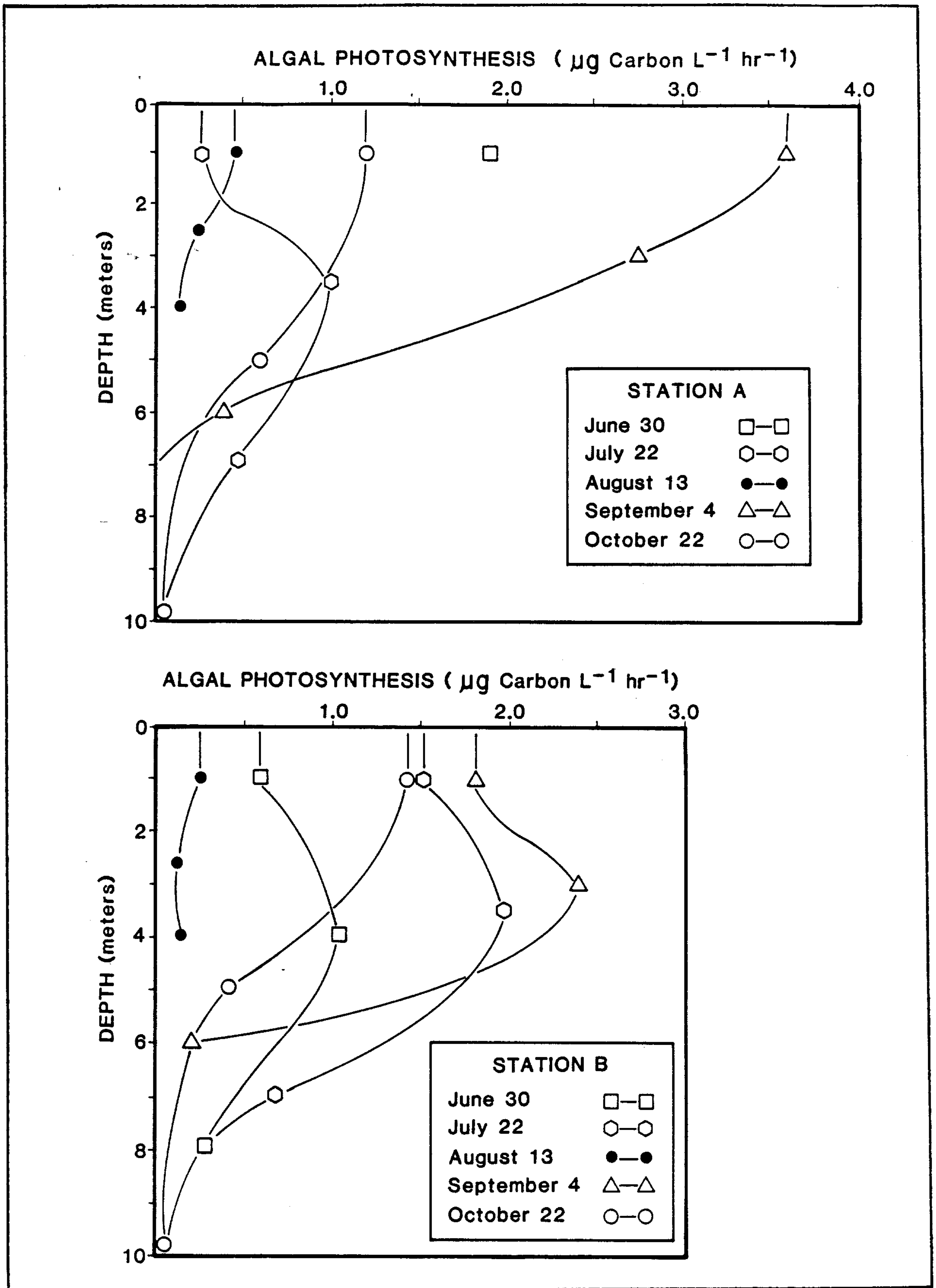

Figure 11. Rates of algal photosynthesis (mg $C/m^3/hr$) by station showing changes in metabolic activity as a function of both photic zone depth and time in 1981.

10 m before and after the glacial influence and to only 4 m during the height of the meltwater intrusion. Daily areal estimates, ranging from 615 mg C/m^2 to 48 mg C/m^2 before intrusion, were reduced to 6 mg C/m^2 - 12 mg C/m^2 during the height of turbidity during August. When the lake began to clear, the daily areal carbon-fixation rate increased from 38 mg C/m^2 to 128 mg C/m^2. Thus, we found that the amount of photosynthetic activity per square meter of lake surface not only depends on algal biomass but also on the rate of algal uptake (on a volumetric basis) at the individual depths throughout the photic zone.

<u>Density of Zooplankters Community Composition</u>

The zooplanktonic community of Crescent Lake is composed of three organisms: *Cyclops scutifer*, *Kellicottia longispina*, and *Asplanchna* sp. Of these, only the macro-zooplankter *Cyclops* is considered to be food for rearing sockeye juveniles. The seasonal abundance pattern of this raptorial feeder was found to be fairly consistent during the three years (1979-1981) that seasonal profiles were completed (Figure 12). In general, the initial overwintering population density (as determined in October) was gradually reduced to minimal population densities by April of the following year. Thereafter, population densities expanded to slightly greater densities in June and July and then erupted to maximal densities in August (Station A) and September-October (Station B). Population densities during the June through October period averaged 111,476 and 134,417/m^2 at Station A and 137,643/m^2 and 105,741/m^2 at Station B in 1980 and 1981, respectively. So although the population densities peaked at slightly different times, the overall numbers of adult copepods at each station in both years were very comparable.

In terms of relative abundance, the predaceous rotifer *Asplanchna* sp. followed the most numerous *Cyclops*. Mean population densities of *Asplanchna* reached 52,305/m^2 (n=6) and 156,908/m^2 (n=6) at

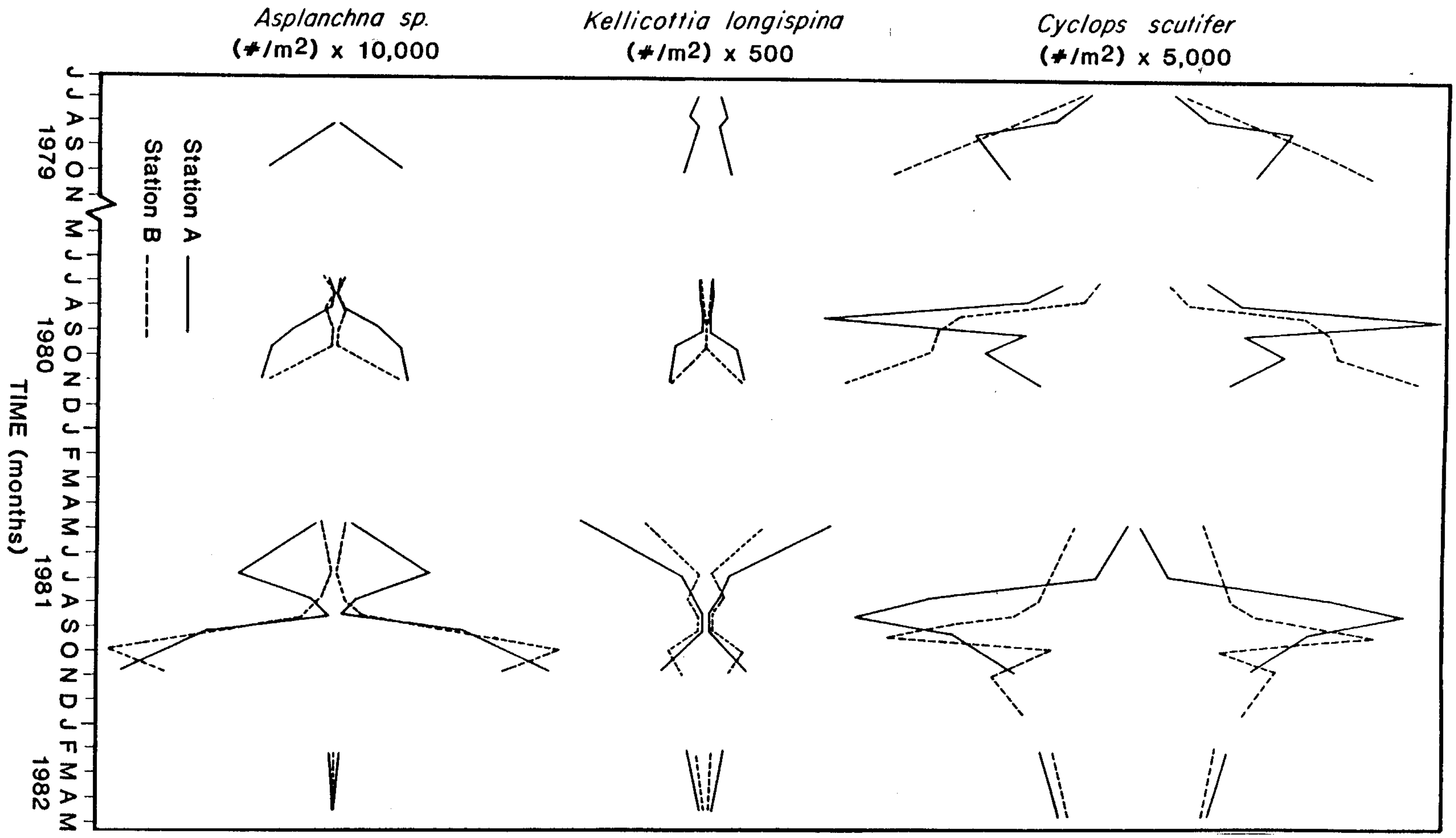

Figure 12. Seasonal density (organisms/m^2) patterns for *Cyclops scutifer*, *Asplanchna* sp., and *Kellicottia longispina*: the primary limnetic zooplankters found within Cresent Lake in 1979, 1980, 1981, and the winter of 1982.

Station A during the June through October period and averaged 23,350/m^2 (n=5) and 125,331/m^2 (n=5) at Station B during the same time period in 1980 and 1981, respectively. The seasonal abundance pattern of *Asplanchna* closely resembled that of the raptorial feeding *Cyclops*. Again, low population densities in the spring and early summer were followed by explosive population increases in September and October. However, unlike *Cyclops*, seasonal population densities of *Asplanchna* were vastly different in 1980, compared with those in 1981. The average number of *Asplanchna* sp. in 1981 (June through October) was nearly 4 times that in 1980, rising from 40,495/m^2 (n=11) to 154,484/m^2 (n=11).

Unlike the predaceous rotifer *Asplanchna*, the herbivorous rotifer *Kellicottia longispina* never achieved large densities. Seasonal means ranged from only 5,069/m^2 (n=11) to 6,551/m^2 (n=11) in June through October of 1980 and 1981, respectively. The density of *Kellicottia* was only slightly higher at Station A, compared to Station B in both years sampled. Mean densities of *Kellicottia* during June through October equalled 5,761/m^2 (n=6) and 6,518/m^2 (n=5) at Station A and 4,239/m^2 (n=5) and 4,898/m^2 (n=5) at Station B during 1980 and 1981, respectively. Peak numbers were found in late winter; the densities then declined through the summer and showed only a slight rise in the fall. The timing of the yearly seasonal peak in the number of *Kellicottia* was less consistent, compared to the timing of peak numbers of *Asplanchna* and *Cyclops*. For example, in April 1981 numbers reached the highest of any sampled date (38,854/m^2); however, in April 1982 numbers were exceedingly low (2,700/m^2).

Since *Cyclops scutifer* is the primary forage available to sockeye fry, its population dynamics (size, sexual maturity, egg production) were studied in some detail (Figure 13). The univoltine *Cyclops* overwintered as small-sized ($\leq$0.85 mm) premature adults (Figure 13a) along with a small number of nauplii. After ice out, the subadults grew until becoming sexually mature ($\leq$0.85 mm), and

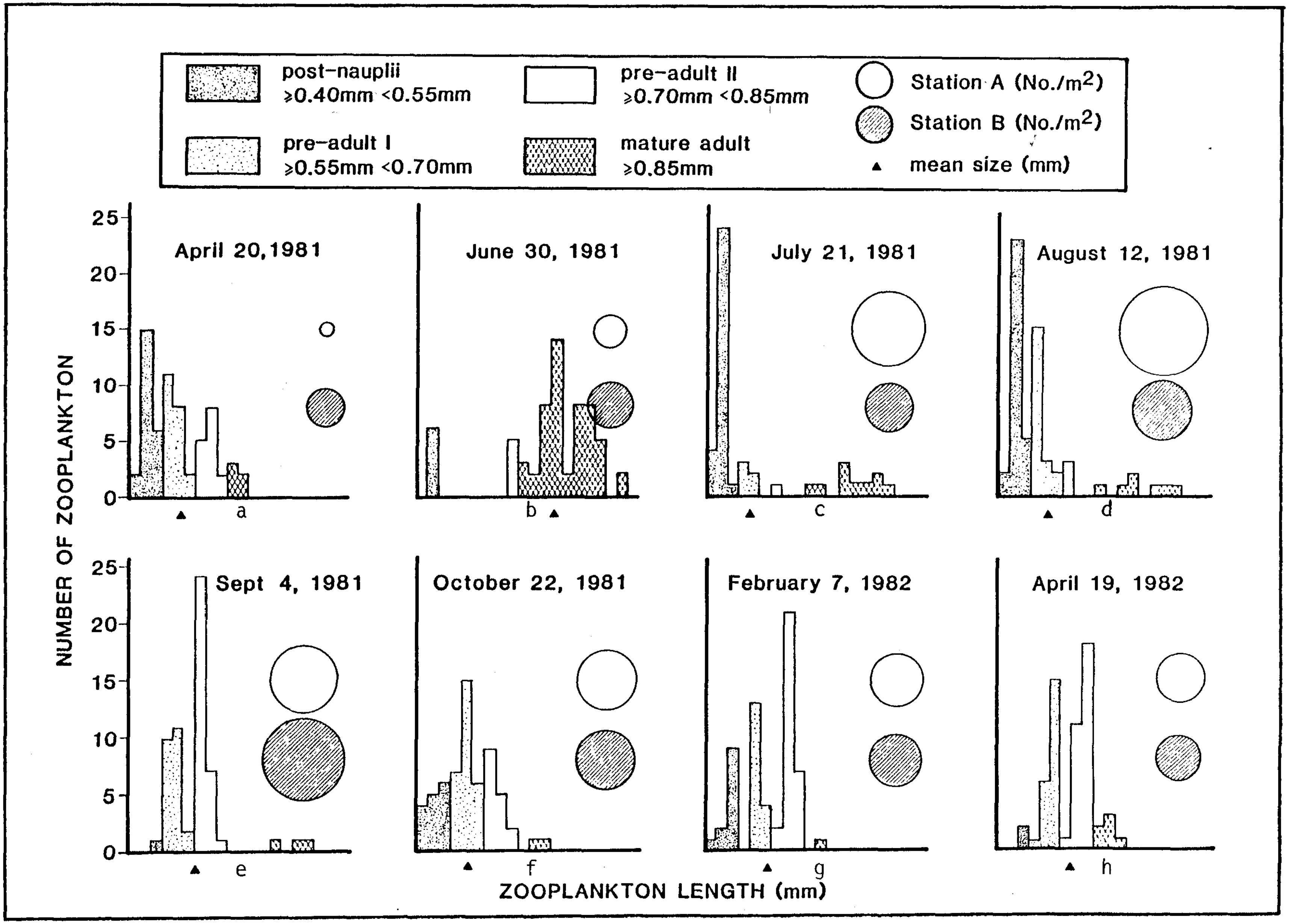

Figure 13. Concommitant changes in density, body size, and developmental stage of *Cyclops scutifer* by date in Crescent Lake in 1981.

by late June, egg sacs began to appear in the females. At this time nearly 80% of the population consisted of mature adults; a few post-nauplii, or subadults, were present (Figure 13, part b). By July the population expanded (Figure 13, part c); nearly 60% of the population consisted of a new year class of post-nauplii (i.e., ≧0.40 mm to <0.55 mm). In addition, the number of large-sized adults (≧0.85 mm) decreased to only 25% of the population, while a month earlier they comprised nearly 80% of the population. In August, maximal egg production took place; it was accompanied by (1) a further decline in the number of larger adults to 14% of the population, (2) a decrease in the smaller size class to 40% of the population, and (3) the emergence of the pre-adult-I size class (≧0.55 mm to <0.70 mm) as the dominate group (Figure 13, part d). By September the larger individuals represented <5% of the population, and the smaller, younger individuals (post-nauplii) represented 2% of the population (Figure 13, part e). At this juncture, nearly 92% of the population was within the pre-adult-I and pre-adult-II stages; 54% were within the pre-adult-II size class (≧0.70 mm to <0.85 mm). Thus, during September/October, the overwintering population began to form, consisting of the three smaller immature adult stages (Figure 13, part f). This structure is reminiscent of the population structure observed in April 1981 and in the spring of 1982 (Figure 13, parts g-h).

Seasonally, a pronounced change in the overall average size of *Cyclops scutifer* developed only in June when the sexually mature adults first obtained their maximal size (Figure 13, part b). After this, both the appearance of small post-nauplii and the disappearance of the larger-size class combined to drastically decrease the average size. Subsequently, the average size of an individual slowly rose as the new-year class moved through progressively older and larger life stages. Finally, *Cyclops scutifer*, like other cyclopoid copepods, is a raptorial feeder, whether the type of food seized is animal or plant, because no filtration mechanism has developed in this group; i.e., the mouth parts are modified for seizing and biting. Food consists of unicellular plants (algae), animals (e.g., small metazoans), and especially other crustaceans, including its own nauplii.

DISCUSSION

Glacier MeltWater Intrusion

The major influence on the fertility of Crescent Lake was the magnitude of glacial meltwater intrusion, which potentially reduced the production achieved within the epilimnion by (1) decreasing the depth of the photic zone, (2) decreasing epilimnetic temperatures, and (3) increasing the flushing rate (thereby decreasing the concentration of available nutrients by dilution). Operating together in the critical summer-to-early-fall period, these processes could depress the productive capacity of the lake. Hence, without invoking a nutrient-limitation hypothesis, Crescent Lake would have all the characteristics of an extremely unproductive oligotrophic system because of the overwhelming influence of physical features.

The timing, as well as the magnitude, of the glacier meltwater is of considerable importance to the biological community within the lake, because initiation of the melt period coincides with the initial pulse of autochthonous production. By foreshortening the spring pulse, major food production for spring-rearing sockeye juveniles could be considerably reduced. That is, cohort recruitment by *Cyclops scutifer* occurred just prior to glacial melt (July). Consequently, forage for the emerging nauplii could be reduced at a time when needed most. Moreover, the impact of glacial particles (1 to 20 m in size) on the macrozooplankton community is not confined to the indirect effects on food supply that potentially limit the number of *Cyclops*. Indeed, the size of the glacial particles overlaps that of the phytoplankton (Porter

1977), which interferes with the nonselective filter-feeding mode of most cladocerans. Thus, by both reducing the density of algal biomass and decreasing the feeding efficiency, glacial particles exclude the cladocerans from the zooplankton community of the lake. This is important since cladocerans are preferred forage items for sockeye fry (Merrell 1964; Foerster 1968; Narver 1970; Goodlad et al. 1974; Jaenicke et al. 1980) when compared to cyclopoids, which are small and very difficult to capture because of a refined ability to escape predators (O'Brien 1979; Drenner and McComas 1980). Thus, the visual-feeding sockeye juveniles are left to forage on a very dilute prey group that consists of a species that rearing juveniles have a difficult time catching, even under the best of conditions.

Maximal glacier meltwater influence on the fertility of the lake was observed to occur in August and September of 1979, 1980, and 1981. At this specific time in each of the three years, the photic zone was indeed drastically reduced (Figures 5 and 6); epilimnetic temperatures were reduced from the July to early August maxima (Figures 3 and 4), and the epilimnion showed slightly lowered concentrations of the specific algal nutrients: inorganic nitrogen and reactive phosphorus (Figures 7 and 9). Prior to late August and September, a significant input of glacial meltwater, beginning in July, initiated the changes noted above. Moreover, the only nutrient that began to increase in concentration by late June was total phosphorus (Figure 9). At the height of the glacier meltwater influence in August or September, TP levels reached 2 to 3 times those found during the spring period.

If the introduction of the glacial water, which began in June, acted to depress primary production by the mechanisms discussed above, then algal productivity should have been reduced during the period of maximal glacial influence; i.e., mid-August through September. Standing crop estimates (chl a) indicated peak algal levels in September at both stations in 1980 and 1981; i.e., consistently after peak inflow of glacier meltwater. Furthermore, in 1980 and 1981 maximal rates of photosynthesis (per m^2) were observed in late July and early September at both stations (*see* Figure 11). However, on 13 August, at the height of the glacial meltwater influence, chl a levels and, in particular, photosynthetic rates (per m^3) were considerably reduced. Moreover, areal photosynthetic rates decreased during August, and photosynthesis per unit of chl a showed minimal values at the height of the meltwater intrusion in August and even during the subsequent sampling occuring late in September. Algal uptake (per m^3) within the shallowed photic zone in September recouped areal productivity (per m^2) to levels comparable to before and after meltwater intrusion only because of a 5-to-8-fold increase in algal biomass (chl a) (Table 2).

While we expected a time-lag in the stimulation of algal biomass that was triggered by the increase in phosphorus loading from glacier meltwater, we also anticipated an increase in the rate of production as well. We did realize an increase in algal biomass (chl a), but only after a time lag of nearly two months following the initial increase in epilimnetic inorganic particulate phosphorus IPP (Figure 10). Using IPP (rock phosphate) as a source of phosphorus, Fitzgerald (1970) and Smith et al. (1977) observed comparable time-lags before algal biomass began to increase. However, areal carbon incorporation rates, as well as volumetric carbon uptake rates per unit chl a, decreased. Similar observations on the effect of glacially derived turbidity on volumetric rates of primary productivity in Naknek Lake, Alaska, were reported by Goldman (1960).

Thus, while the fertility of the epilimnion increased, as indicated by increasing chl a levels and decreasing levels of inorganic phosphorus, the actual primary productivity, or rate of production within the euphotic zone, dramatically decreased. The presence of a large increase in non-particulate phosphorus within the dark hypolimnion and the absence of that increase within the euphotic zone can be accounted for not by an increase loading of phosphorus within the hypolimnion but by equal loadings to both strata that are accompanied by algal uptake of reactive phosphorus within the remaining photic zone.

Photic Zone Volume: Comparisons Across Lake Types

The magnitude of the photic volume is of concern because light penetration powers the photosynthetic process, which is the basis of the autochthonous food chain. Similar photic zone changes, caused by glacier meltwater input, resulted in decreased primary and secondary production within Owikeno Lake, British Columbia (Ruggles 1965). Specifically, a low-water transparency exerted a major influence on lake productivity, resulting in a low standing crop of zooplankton and an extremely low growth rate and summer survivorship of lake-rearing sockeye juveniles. In this regard, the seasonal photic volume of Crescent Lake compares favorably with other lake systems (Table 3). Consequently, the decrease in light penetration caused by glacier meltwater serves to reduce the euphotic zone volume of large glacial systems to levels comparable to smaller clear-water sockeye systems. For example, Tustumena Lake is 270 times the size of Hidden Lake by total volume and is 33 times greater by surface area, but both lakes have essentially the same euphotic zone volume. Likewise, the entire volume of Crescent Lake is 3 times that of Hidden Lake, while the surface area of Crescent Lake is 2.5 times that of Hidden Lake; yet both lakes have comparable euphotic volumes. Because a vast majority of Alaska sockeye systems are within the same broad trophic classification (oligotrophic), a consideration of euphotic zone volumes may be a more meaningful comparison, in terms of the biomass produced, than the mere surface area considerations.

Nutrient Demand and Supply

In regard to phosphorus loading (supply), Crescent Lake is classified as oligotrophic (Figure 14, part A), and it fits well within

Table 3. Comparison of sockeye nursery lakes by lake type (water clarity) emphasizing the general lowering of the light compensation point and euphotic volume within the glacially influenced and organically stained systems relative to clear water lakes lying within the same range of size, total volume, and water exchange rates.

Lake	Volume ($m^3 \times 10^{+6}$)	Lake type (water clarity)	Surface area ($m^2 \times 10^{+6}$)	Surface area (acres)	Water residence time (yr)	Light compensation level (m)	Euphotic volume ($m^3 \times 10^{+6}$)	Euphotic volume (% of total)
Trail Lakes	124	Glacial	8.1	1,754	0.19	0.5	3.6	3
Tustumena	37,000	Glacial	295.0	73,944	17.20	1.0	295.0	<1
Skilak	N.A.	Glacial	99.0	24,463	N.A.	1.5	148.5	<1(est.)
Kenai	N.A.	Glacial	56.0	13,837	N.A.	4.0	224.0	<1(est.)
Crescent	98	Semi-Glacial	3.3	805	0.2	8.0	26.4	27
Eklutna	512	Semi-Glacial	14.0	3,458	1.8	3.0	42.0	8
Ptarmigan	125	Semi-Glacial	3.0	750	1.1	6.0	15.6	17
Crescent	389	Semi-Glacial	16.2	4,002	0.3	5.5	89.1	23
Bakewell	67	Organic Stain	2.8	692	--	4.5	12.6	19
Hugh Smith	198*	Organic Stain	3.2	800	1.1	5.0	16.0	8
Packers	26	Organic Stain	2.1	519	3.0	4.0	8.4	32
McDonald	197	Organic Stain	4.2	1,035	0.7	7.5	31.5	16
Falls	30	Organic Stain	1.0	254	0.5	9.5	9.0	29
Bear	19	Clear	1.8	445	0.8	9.5	17.1	90
Hidden	138	Clear	6.8	1,680	11.2	15.0	102.0	74
Upper Russian	122	Clear	4.6	1,137	1.1	13.0	51.0	42
Karluk	1,920	Clear	39.0	9,637	6.0	20.0	780.0	41
Tokun	38	Clear	1.8	448	1.0	16.0	25.0	65
Eshamy	122	Clear	3.6	890	2.7	20.0	72.0	59
Leisure	23	Clear	1.1	259	0.3	18.0	19.8	86
Larson	29	Clear	1.8	445	1.7	9.5	17.1	59
Sea Lion Cove	0.32	Clear	0.08	19	0.3	6.9	0.26	80
Nunavauguluk	4,489	Clear	79.0	19,513	6.0	25.0	1,975	44
Cultus	201	Clear	6.3	1,550	N.A.	23.0	145	72

*Volume of the mixolimnion

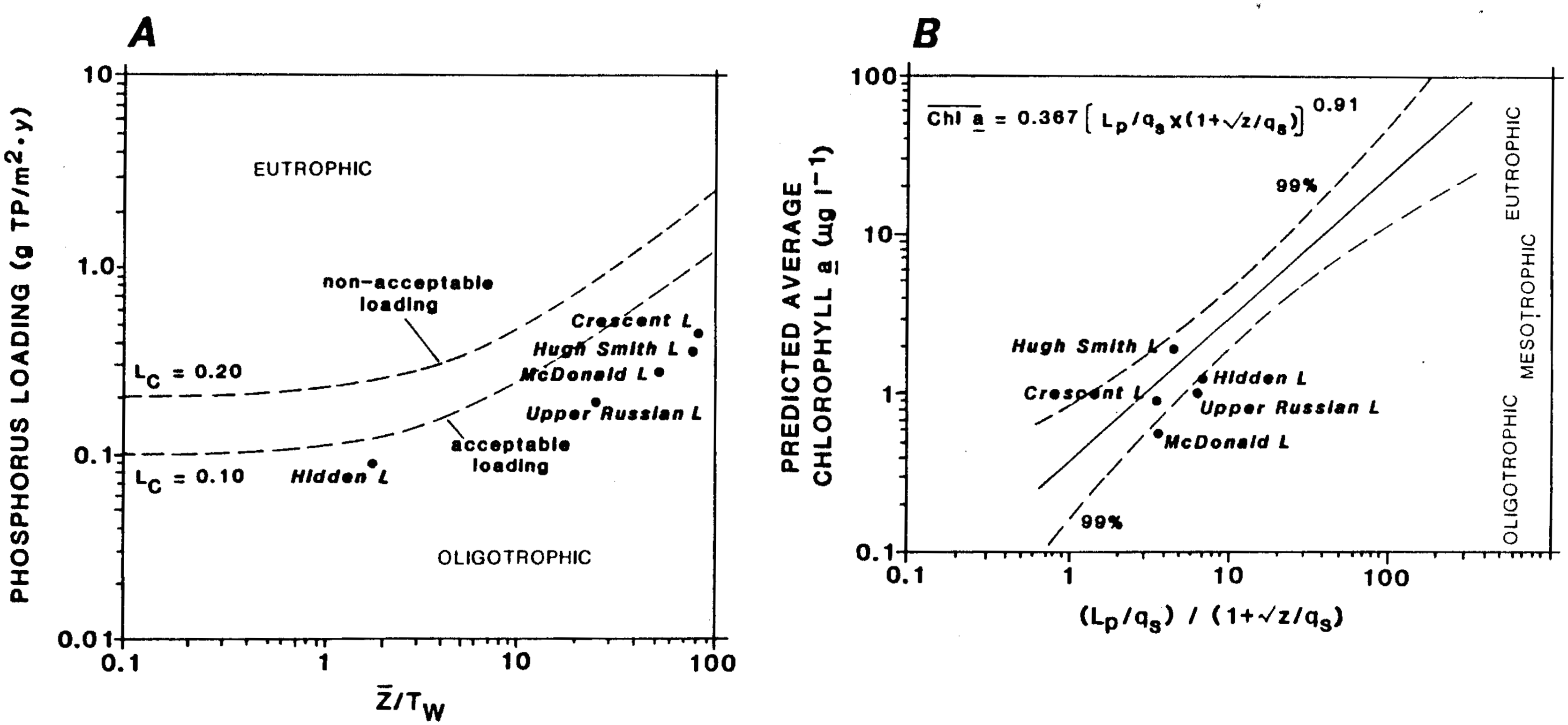

Figure 14. Phosphorus loading characteristics of several oligotrophic Alaska lakes and the relationship between phosphorus concentration and resultant summer chlorophyll a production [after Vollenweider (1976)].

a total phosphorus summer chl a response model (Figure 14, part B) obtained by Vollenweider (1976). In order to fit within the latter relationship, phosphorus is required to limit system production; i.e., an increase/decrease in phosphorus loading results in a direct and proportional increase/decrease response by the phytoplankton. This is based on a demand/supply relationship for the primary nutrients (C, Si, N, P); i.e., the nutrient with the highest demand per supply controls production. In general, the nutrients C, Si, N, and P are in demand by phytoplankton at atom ratios of 106:17:16:1, respectively. In Crescent Lake, C:Si:N:P supply ratios are 320:380:91:1; these are a clear indication of the importance of phosphorus supply to autochthonous production; i.e., demand/supply values of P=1.00, C=0.33, N=0.18, and Si=0.05.

Phosphorus Sources and Losses: Comparison of Sockeye Nursery Lakes

Lakes differ in morphometric features (e.g., mean depth, surface area, and flushing rate or water residence time [Table 4]) that combine to define the supply of nutrients; i.e., phosphorus to lake systems. Like euphotic zone volume, these features fluctuate from lake to lake; e.g., mean depth varies from 71 to 20 m and water residence time ranges from 0.3 to 11.3 yr. Such variation results in the well-known differential fertility of lake systems. The empirical relationship that binds these factors together into a predictive tool was developed by Vollenweider (1976), who developed phosphorus-loading criteria from this model; i.e., the surface specific loading (Lp) and the surface critical loading (Lc). The former (Lp) describes the present phosphorus loading rate; the latter (Lc) describes the loading rate not to be exceeded, in order to prevent unwarranted change in preexisting lake-water quality. Again, vast differences were found between sockeye nursery lakes (Table 4), because existing surface specific loading rates ranged from 53 mg $P/m^2/yr$ to 650 mg $P/m^2/yr$. A third term (Lf) is introduced here for specific use in salmon nursery lakes, and it is defined as the phosphorus loading from decaying salmon

Table 4. Comparison of surface specific yearly loading (Lp), surface critical loading (Lc), and salmon carcass loading (Lf) of phosphorus in several Alaskan lakes.

Parameter	Date: 1981 Lake: Crescent	1980 Upper Russian	1980 Hidden	1980 Hugh Smith	1982 McDonald
Area ($x10^{+6}$ m^2)	16.2	4.6	6.8	2.9	3.4
Volume ($x10^{+6}$ m^3)	389.0	122.0	138.0	208.5	123.0
Mean Depth ($\bar{z}$)(m)	24	27	20	71	37
Water Residence Time (yr) (Tw)	0.3	1.1	11.3	0.9	0.6
$\bar{z}$/tw (qs)	80	24.6	1.8	77	53
Lp (mgP/m^2/yr)	458	276	53	650	373
Lc (mgP/m^2/yr)	1,238	503	77	1,512	691
Lp/Lc	.37	.55	.68	.43	.54
Lf (mgP/m^2/yr)	50.0	181.0	5.2	33.0	342 .0
Lf/Lp	.13	.66	.10	.05	.92
Escapement	90,000 (sonar)	125,000 (weir)	5,000 (weir)	<10,000 (weir)	129,000 (weir)
Escapement/m^2	.006	.027	.0007	.003	.038

carcasses. As such, fish loading (Lf) is a subfunction of surface specific loading (Lp), and it, too, changes from lake to lake, ranging from 5.2 mg P/m^2/yr to 342 mg P/m^2/yr. However, even though Lf is part of Lp, they are not directly related; i.e., Lf and Lp can rise and fall independently of each other.

For the lake systems discussed, present loading (Lp) of phosphorus extended from 37% to 68% of critical loading (Lc). Of the present phosphorus loading (Lp), Lf represented from 5% to 92%; that is, the fertility of lakes that receive a significant nutrient income (as a percent of Lp) from a fall escapement of salmon (e.g., Upper Russian Lake) could be tied to the increase or decrease in the number of decaying fish carcasses. If a decrease in the number of spawning fish repeats itself over many years, a lake can be drastically reduced in fertility. However, since Lf and Lp can rise and fall independently, a short fall in Lf can be made up by a greater Lp. Thus, oscillations in lake fertility can arise by not only changing Lf but also by changing Lp. Concurrent decreases or increases in Lp and Lf result in minimal and maximal phosphorus loading rates, respectively; directly coupled with the fluctuations in P-loading are resultant increases or decreases in lake fertility.

Nutrient-loading rates (Lp) change by alterations in edaphic (e.g., logging a watershed) and climatic (e.g., rainfall) influences. However, a long-term decrease in Lf can also lower the amount of nutrients delivered to a system by a definable amount. As an example, Hugh Smith Lake has a Lp of 650 mg P/m^2/yr (Table 4). Presently, 5% of Lp is supplied by Lf from an escapement of <10,000 sockeye adults. On a yearly basis, 1,901 kg P enters Hugh Smith Lake (Figure 15); 5%, or 96 kg P, comes from the adult escapement, and 95% enters from other sources; e.g., the sediments and/or watershed. Losses of phosphorus from the lake include the 2 kg lost by the smolt migration. Thus, adult fish import considerably more nutrients to the lake than are lost by the migrating smolts. In contrast, 978 kg P are lost annually by drainage of Hugh Smith Creek: an amount equal to nearly 49% of the P annually entering the lake. Thus, a major portion of the phosphorus lost from the system leaves via the outlet. This flushing continues year after year, regardless of the magnitude of Lf, and coupled with a decrease of Lf, it is the major cause of decreased lake fertility.

Historical escapements of sockeye into Hugh Smith Lake have been placed at approximately 100,000 adults. Historically, instead of Lf equalling 5% of Lp, as is presently the case, Lf equalled 34% of Lp (given that the other components of Lp were roughly equal then and now). Increasing Lf from 5% to 34% of Lp should increase the fertility of Hugh Smith Lake. Thus, in 1980 the nutrient equivalent of 100,000 sockeye (310 mg $P/m^2/yr$) was added to Hugh Smith Lake through a lake-fertilization program.

Finally, the pattern of nutrient supply and removal places upper and lower limits on productivity (lake fertility) and is found in diversified combinations in Upper Russian, Hidden, and Crescent lakes. In essence, all lakes metabolize phosphorus differently (Figure 15), but the dissimilarity of considerable importance to Crescent Lake is the flushing rate. Much of the phosphorus annually entering the lake (6,237 kg P) is transported out of the lake (6,135 kg P) via Crescent River (especially the non-BAP connected with the glacial silt). In contrast, Hidden Lake, which has a much longer water residence time, exports very little (84 kg P) of the 359 kg P entering the lake. That is, Crescent River exports 98% of the annual areal phosphorus load compared to only 34% for Hidden Creek. Such a reduced residence time for phosphorus in the Crescent system reduces the efficiency or effectiveness of a unit expression of phosphorus as chl a.

Phosphorus levels have not only been linked to increased production of chl a in temperate-zone lakes (Dillon and Rigler 1974; Vollenweider 1976; Smith 1979) but also to increased fish yields

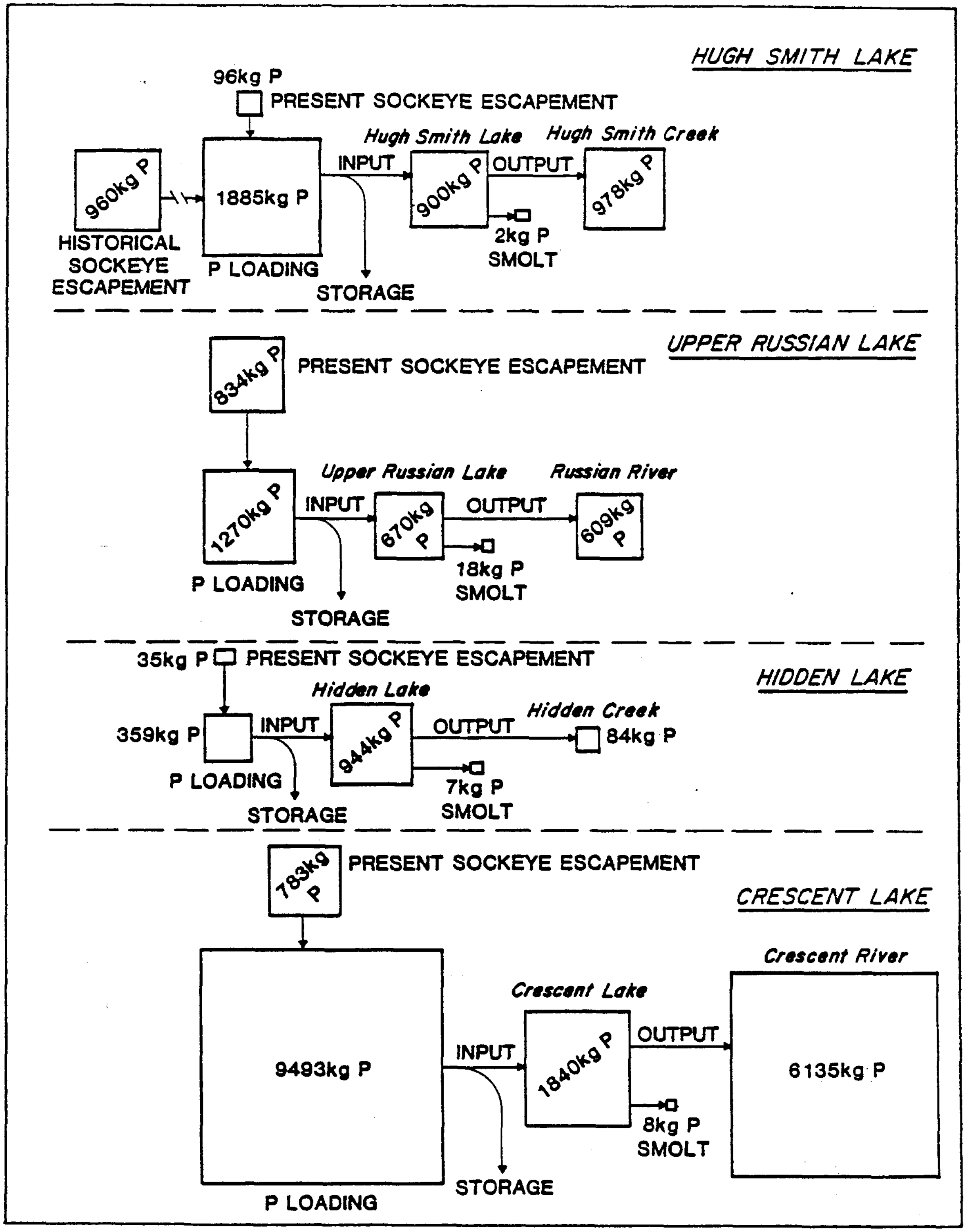

Figure 15. Compartmental representation of yearly phosphorus budgets for several Alaskan lakes showing magnitudes of phosphorus input and outflow relative to total lake phosphorus (size of compartments are proportional to phosphorus content).

(Hanson and Leggett 1982). In addition, photosynthesis has been correlated with increased fish yields (Melack 1976; McConnell et al. 1977) and even with increased sockeye smolt production (Nelson 1958). As such, the linkage between total phosphorus and primary production and then between primary production and fish yield has been established.

RECOMMENDATIONS

Nutrient Enrichment

Irregularities were noted in the temperature and light regimes at Stations A and B in both 1980 and 1981, suggesting a variable effect of the glacier meltwater on the two stations. This, in turn, suggests a pattern of water flow (Figure 16) from the major glacial tributary stream that, in large part, bypasses the upper third of the lake (i.e., Station B). Thus, the water-retention time of the upper third of the lake may be considerably greater than that of the lower two-thirds of the lake.

In addition, representative temperature profiles (Figure 17) indicate a period of epilimnetic thermal stability between the latter part of June through the first week in September, or approximately 10 weeks. This period of time coincides with minimal algal and zooplankton standing crops, decreasing nutrient levels, and the period of emergence of a new crop of immature zooplankton. In addition, the end of the proposed fertilization period (early September) coincides with maximal glacier meltwater influence and is the point at which the system can carry itself; i.e., preexisting production should be relatively high. Thus, fertilization is recommended for the upper third of the lake, including Station B but excluding Station A and Station C (added in 1982), with application taking place once a week for 10 weeks (Figure 18).

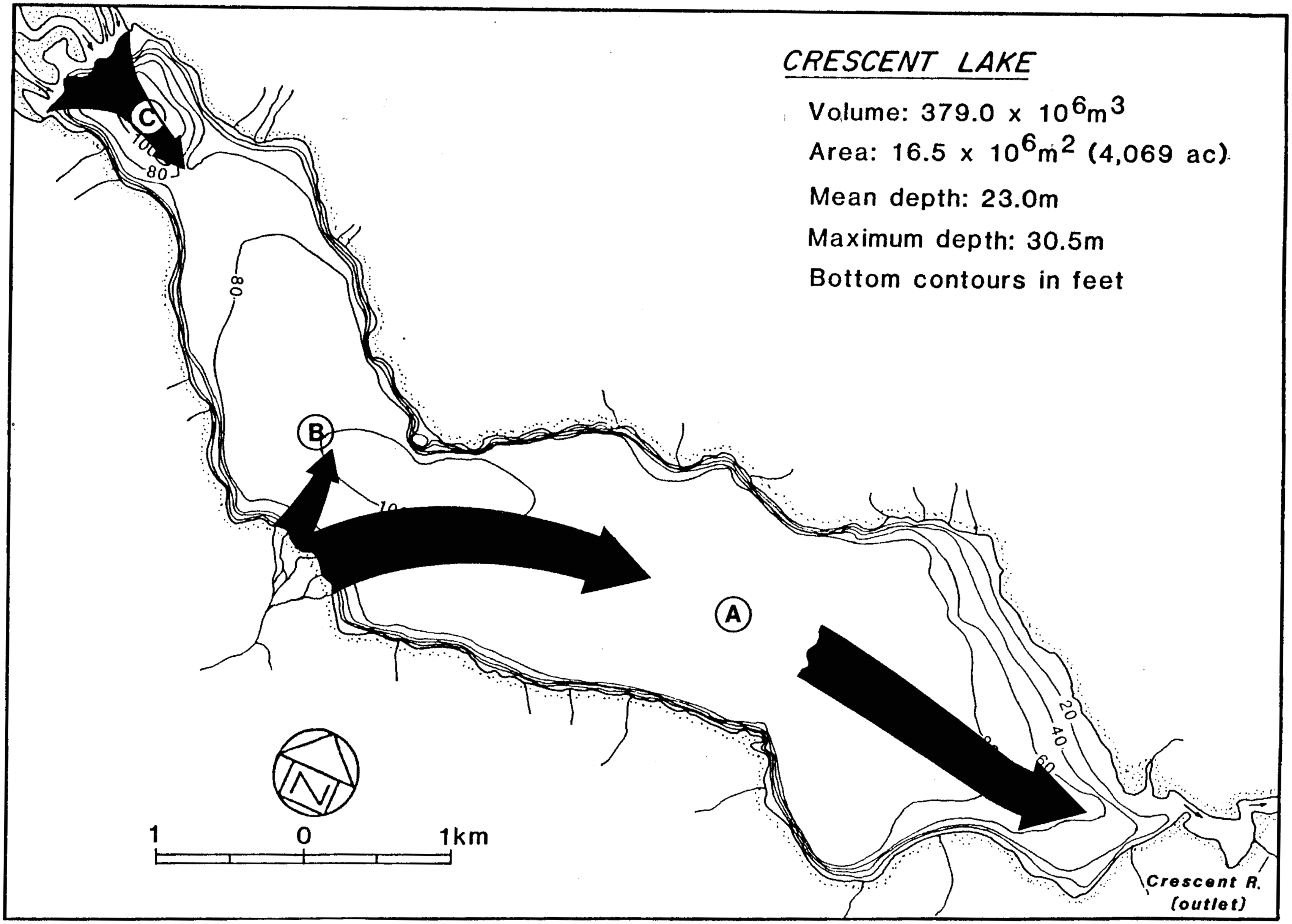

Figure 16. The major inflow flow pattern for glacier meltwater intrusion into Cresent Lake.

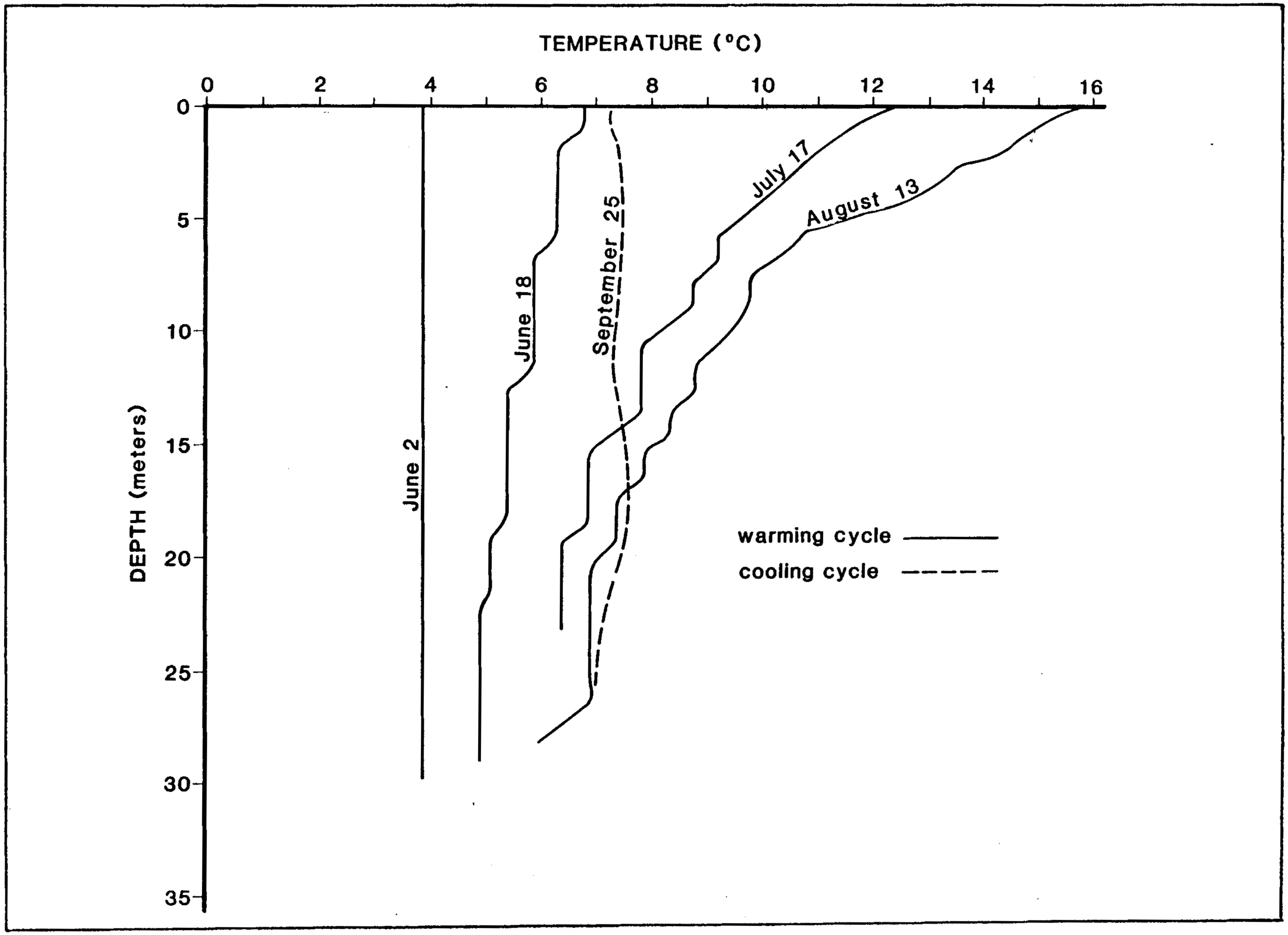

Figure 17. Temperature profiles showing heating and cooling cycles and thermal stratification in Crescent Lake in 1979.

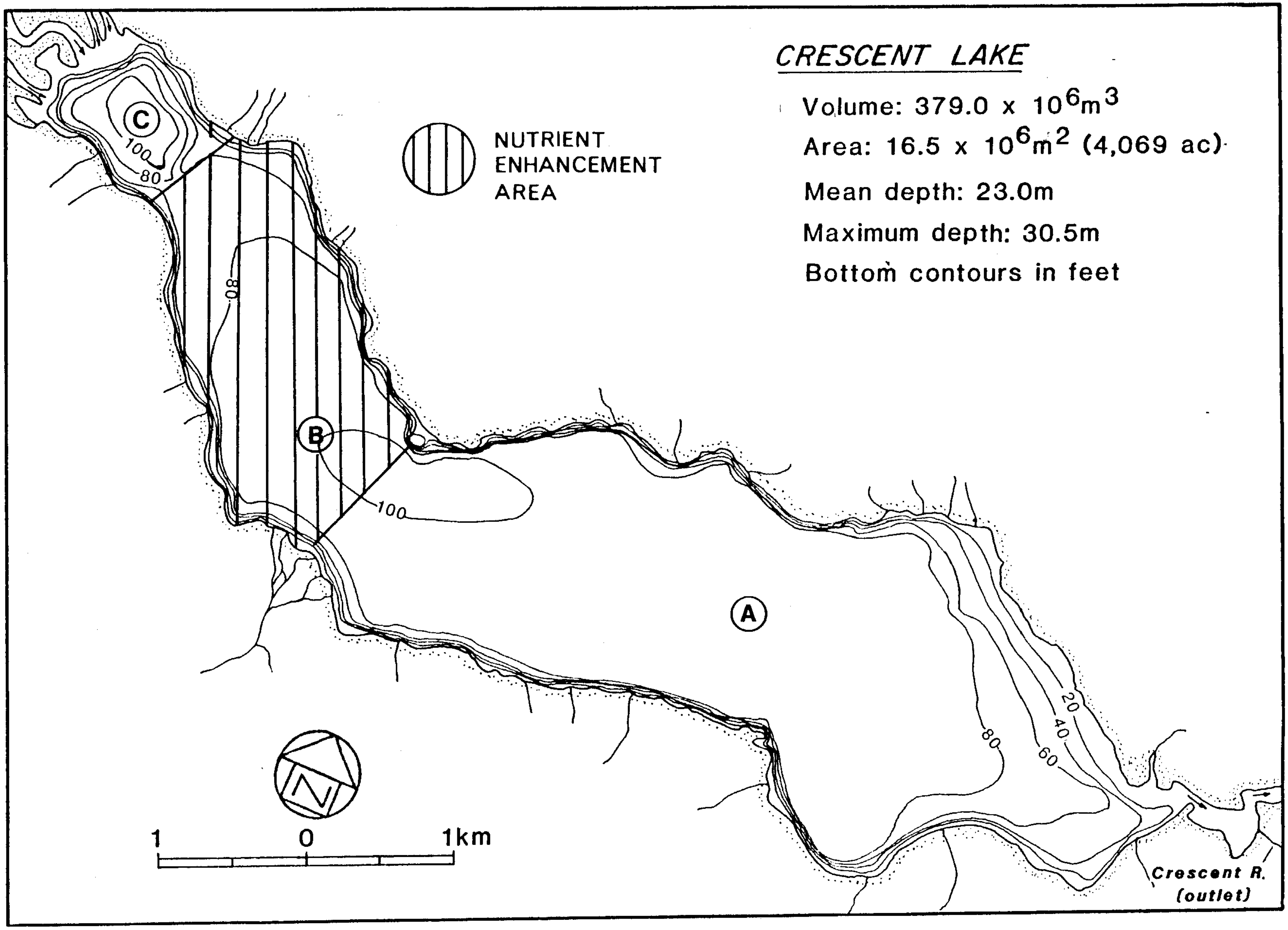

Figure 18. Proposed fertilization zone for 1982 nutrient enhancement experiment within Crescent Lake.

Nutrient Loading

The present phosphorus loading (Lp) to Crescent Lake is estimated at 200 mg $P/m^2/yr$; the critical rate of loading (Lc) is estimated at 572 mg $P/m^2/yr$. We recommend increasing Lp to a level equal to 75% of the Lc, which requires 3,770 kg P. Using a 27-7-0 fertilizer ($N-P_2O_5-K$) that delivers an N:P atom ratio of nearly 18:1, this rate of addition requires the application of 23,560 gal of product containing 0.16 kg P/gal. With an application period of 10 weeks, 2,356 gal/week or 336 gal/day are required.

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