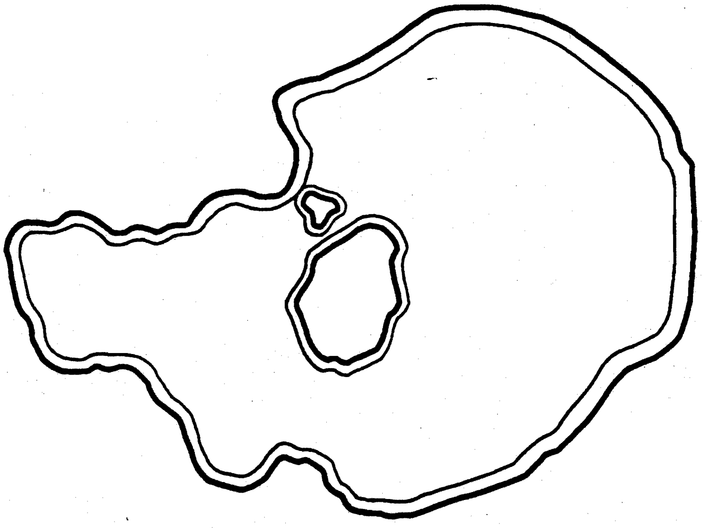
An Auxiliary Report
Prepared for the

MONO BASIN WATER RIGHTS EIR

Mono Lake Benthic Ecosystem Research: Aquatic Productivity Component of the Environmental Impact Report



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Mono Basin EIR Auxiliary Report No. 8

An Auxiliary Report
Prepared for the
Mono Basin Water Rights EIR Project

This auxiliary report was prepared to support the environmental impact report (EIR) on the amendment of appropriative water rights for water diversions by the City of Los Angeles Department of Water and Power (LADWP) in the Mono Lake Basin. Jones & Stokes Associates is preparing the EIR under the technical direction of the California State Water Resources Control Board (SWRCB). EIR preparation is funded by LADWP.

SWRCB is considering revisions to LADWP's appropriative water rights on four streams tributary to Mono Lake, Lee Vining Creek, Rush Creek, Parker Creek, and Walker Creek. LADWP has diverted water from these creeks since 1941 for power generation and municipal water supply. Since the diversions began, the water level in Mono Lake has fallen by 40 feet.

The Mono Basin water rights EIR examines the environmental effects of maintaining Mono Lake at various elevations and the effects of possible reduced diversions of water from Mono Basin to Owens Valley and the City of Los Angeles. Flows in the four tributary creeks to Mono Lake and water levels in Mono Lake are interrelated. SWRCB's decision on amendments to LADWP's water rights will consider both minimum streamflows to maintain fish populations in good condition and minimum lake levels to protect public trust values.

This report is one of a series of auxiliary reports for the EIR prepared by subcontractors to Jones & Stokes Associates, the EIR consultant, and contractors to LADWP. Information and data presented in these auxiliary reports are used by Jones & Stokes Associates and SWRCB, the EIR lead agency, in describing environmental conditions and conducting the impact analyses for the EIR. Information from these reports used in the EIR is subject to interpretation and integration with other information by Jones & Stokes Associates and SWRCB in preparing the EIR.

The information and conclusions presented in this auxiliary report are solely the responsibility of the author.

Copies of this auxiliary report may be obtained at the cost of reproduction by writing to Jim Canaday, Environmental Specialist, State Water Resources Control Board, Division of Water Rights, P.O. Box 2000, Sacramento, CA 95810.

MONO LAKE BENTHIC ECOSYSTEM RESEARCH:

AQUATIC PRODUCTIVITY COMPONENT
OF THE
ENVIRONMENTAL IMPACT REPORT

submitted by

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INTRODUCTION

Evaluating the effects of stream diversion on the Mono Lake ecosystem requires information on the response of organisms and ecological processes to changes in salinity, lake level, and associated environmental features. Although information is available to address some of these issues, further development of predictive models and experimental validation was needed for use in ecological impact assessment. The research reported here consists of three interrelated projects:

(1) population production studies of the aquatic life stages of the alkali fly, consisting of field density data, used to calculate production under current conditions and extended to model altered conditions of salinity and lake level

(2) timing and extent of the drift of aquatic stages of the alkali fly onto the open water surface of Mono Lake, where it becomes available as an important food source to birds (e.g. phalaropes)

(3) experimental micro-ecosystem (microcosm) studies of the effect of salinity on production of the alkali fly

The alkali fly, Ephydra hians, is the central subject of these studies and serves as an indicator organism of habitat quality since it is the primary food source to many Mono Lake birds.

Benthic Habitat and Inhabitants

The physical environment of the lake bottom can be broadly described as consisting of either hard or soft substrates. Like marine intertidal communities, most benthic life in Mono Lake resides in the more stable and structurally complex rocky areas. These rocky areas are primarily tufa groves and tufa-coated pumice blocks, and to a lesser extent pumice stones, mineral crusts (gaylussite), sand conglomerate, and alluvial cobble or gravel. Alkali fly larvae, and particularly pupae, use these substrates as sites for attachment and refuge from water turbulence. During periods of rising lake level, submerged terrestrial vegetation may be similarly used. Soft substrates include deposits of sand, mud, and detritus (decomposing organic matter). Larvae and pupae are most abundant in shallow water (< 1 m depth) though the zone within which they occur extends to between 10 and 15 meters depth, coincident with the thermocline. This defines the littoral-profundal boundary of benthic habitat.

Though the alkali fly is the dominant benthic invertebrate, six other benthic insects can also be found, all dipteran larvae. These include two stratiomyids (soldier flies), two ceratopogonids (biting midges), a dolichopodid (long-legged fly) and a tabanid (deer fly). Only the ceratopogonids and dolichopodids are common. In addition to these insects is a varied microbial community composed of diatoms, filamentous green and blue-green algae, protozoans and bacteria. These often grow as a cohesive mat on sediments or as a layer on rock surfaces, and constitute the primary food source of alkali fly larvae and pupae.

Previous Research and Context for Current Studies

Published information on benthic organisms at Mono Lake that could be used in preparation of the EIR include studies of population ecology (Herbst 1988, Herbst 1990), physiology of osmotic and ionic regulation (Herbst et al. 1988, Herbst and Bradley 1988, Herbst and Bradley 1989a), and algal salinity tolerance (Herbst and Bradley 1989b). Field studies have established the substrate and depth distribution of fly larvae and pupae (Herbst and Bradley 1992), from which a habitat-based population model has been derived. Unpublished studies of salinity effects on the growth, development, and life history of the alkali fly have also been conducted by Herbst and

Bradley. These laboratory studies, done over a wide range of salinities, show reductions in larval growth rate, survivorship, the size and viability of pupae and adults, and reproductive potential as salinity level is increased. Salinities of 150 to 200 g/L and above are lethal, especially to early instar larvae. Algal growth is also inhibited by increased salinity. Such growth-limiting effects are observed over a range of salinities including levels at and below the salt concentration of Mono Lake before water diversions began, not simply above the present salinity. These laboratory studies are designed such that all variables but salinity are controlled, thus isolating osmotic and ionic effects on the species being tested. What these organism-based physiological studies have failed to do is examine the effect salinity has on the entire interacting community of organisms that inhabit the benthic environment. This composite ecological effect of salinity on benthic production was examined in the experimental microcosm studies reported here.

Microcosms are essentially micro-ecosystems that are used to simulate the natural environment, and like large aquariums, can be manipulated to study the effect of changing one environmental factor on the many interacting parts of the ecosystem. Studies of salinity effects on salt lake communities have been conducted only once before using large-scale microcosms. Those were studies of fish and invertebrates at Pyramid Lake, and were instrumental in establishing the limitations of salinity on the biota of this saline lake (Galat et al. 1988).

The microcosm experiment provides an ecological simulation that best approximates the influence of salinity on the productivity of the alkali fly and its associated benthic community. The range of salinities examined allows both prediction of the potential effect of higher salinities, and reconstruction of historical conditions in Mono Lake of the past. The relative changes in productivity and species composition will also provide guidelines for evaluating the the range of salinities that are optimum for yield or sustain community integrity. This defines one set of limits for lake level management and improves the realism of evaluating how salinity affects Mono Lake beyond assessments based on laboratory studies of isolated organisms. In addition, the microcosm studies provide an independent means of validating the predictions of the production model developed from field density data.

Although standing stock estimates of density have been made in previous years (1986-1990), population production of _Ephydra_ _hians_ has not been previously measured. Frequent sampling at six stations around the lake from spring into fall 1991 permitted calculation of secondary productivity based on the method of Kimmerer (1987). This data provides not only a monitoring baseline, but a framework for deriving a predictive production model. Since calculation of production involves larval growth rate terms that are modified by salinity, and abundance terms that are modified by the availability of different habitat types at different lake levels, production could be modeled for specified salinity and lake level conditions.

Along with the population density and production estimates derived from shallow littoral sampling stations, the distribution and timing of larval and pupal drift into the open surface waters of Mono Lake was also surveyed in 1991. When, where, and how much of this drift accumulates provides a connection between fly production and the feeding ecology of phalaropes. Separate studies of prey density food limitation (M.Rubega of UC Irvine) were used to evaluate the adequacy of drift as a food source.

METHODS

(1) Population Density and Productivity

Littoral benthic sampling was conducted every 2-3 weeks from late April until mid-October of 1991. Samples of both hard and soft substrates (8 replicates each) were collected at six stations around Mono Lake (Figure 1). Hard substrates included tufa, pumice, sand conglomerate, and often had surface deposits of gaylussite crystal. Large squares of 200 micron mesh Nitex netting (fine enough to retain eggs) were used to enclose and remove hard substrates from underwater. Rock size varied from 5 to 20 cm in diameter. Soft substrates were varied mixtures of mud, sand and detritus. Samples of this sediment were taken using an 8 cm diameter coring tube. The corer was pushed 2-5 cm deep into the substrate, a broad-blade plastic putty knife slid under the base of the tube, and the core removed intact. The upper sediments were then removed with a large suction pipet and transferred to a mesh storage bag. All samples were taken from a depth of 25 to 50 cm. Sampling was initiated at an arbitrary location and subsequent samples taken 3 to 5 meters away in undisturbed areas. Temperature and specific gravity were also recorded during each sampling, along with qualitative notes on water clarity, substrates present, and the shoreline density of alkali fly adults. Samples were kept refridgerated until processing.

Samples were processed by immersion in buckets of saturated salt solution, floating off the unattached low density eggs, larvae and pupae. Rocks were then immersed in containers of hot tap water, driving hidden larvae out from interstitial spaces. Finally the rocks were closely inspected and any remaining larvae or attached pupae picked off. Larvae and pupae collected in this way, along with the filtered flotation solution, were boiled briefly and preserved in

80% ethanol with 5% glycerol added. Eggs, three larval instars, full and empty pupa cases were counted and densities calculated based both on the surface contours of rocks (three-dimensional area) and their planar projection (two-dimensional outlined area). Wrapping the surface with aluminum foil or tracing outlines onto foil provided the means for estimation of these areas. Foil weights were converted to area equivalents.

(2) Open Water Drift

Third instar larvae, pupae and adults floating on the water surface were sampled using a boat-towed floating net. The net was 75 cm in diameter, held perpendicular to the water surface by floats attached at 2 of 3 bridle rings. This gave the net a 65 cm surface sampling width and a submerged area of 0.355 square meters, down to a depth of 55 cm. A current meter in the mouth of the net was used to gauge distance and volume sampled. Sample stations correspond to the locations used for UCSB plankton surveys (Figure 1). The surface tows (one at each of 10 stations) were conducted in conjunction with these biweekly plankton surveys, from May through October. Tows were typically 3 minutes in duration, covering 50-100 meters distance. In addition to these biweekly surveys, a separate series of near-shore transects were made through phalarope feeding areas (northeast lake) during the peak of their residence (in cooperation with M.Rubega).

(3) Microcosm Salinity Experiments

Salinity effects on the productivity and species composition of the benthic community of Mono Lake is the subject of this large-scale ecological simulation. The experiment consisted of 20 500 L tanks that were filled with Mono Lake water and gradually adjusted to target salinities of 50, 75, 100, 125 and 150 (160 final) g/L total dissolved solids, with each salinity level replicated four times (Figure 2 - tank array). Tanks were made of fiberglass, 4'x4' square and 2' deep (effectively 1 meter square by 50 cm deep). Before use, the tanks were soaked, rinsed and scrubbed inside with freshwater, and painted outside with white water-seal paint to both avoid leakage and moderate solar-heating. On June 20, 1991, Mono Lake water was pumped through a 200 micron mesh filter into all tanks, to a depth of 40 cm. Salinities were gradually diluted (by removal of some lake water) or evaporated over a five week period (daily evaporation rates of 5-10 mm) and evaporate replaced either with lake water or stream water from nearby Lee Vining Creek. During this time, 10 L of sand was added to each tank, followed by 2 L of mixed sediments containing algae and aquatic invertebrates for acclimation. Upon reaching the target salinities, tanks were further inoculated each with 5 L of Mono Lake sediments (algal mat and eggs/larvae of the alkali fly from the Old Marina), and external colonization sources introduced in the form of 0.5 L per tank of sediments collected from both less saline (Black Lake - ca. 50 g/L) and more saline (north shore hypersaline ponds at Mono Lake - ca. 150 g/L) habitats. In order to monitor growth and colonization of hard substrates within the microcosms, standard-sized (10x7x4 cm) rough-textured concrete blocks were cast, soaked in freshwater, and 50 placed over the bottom of each tank (covering about 40% of the total bottom area). These and sand-sediment cores (4 cm diameter) were removed at approximately 1 and 2 months (ten replicates/tank) after initiation of the experiment. Tanks were also equipped with air-lift aerators driven by a single air pump, powered by photovoltaic panels charging a deep-cycle battery system. The air pump operated through a remote timer on daily cycles of 16 hours on and 8 hours off. This aeration, along with the typical 15-25 C daily temperature cycle, provided water circulation and oxygenation. Though water was slightly turbid in elevated salinities at first, aeration also clarified water in all tanks. At initiation of the experimental period (early August) each tank was enclosed within a tent of 1 mm mesh, trapping emerging adult flies and preventing external colonization by insects, or predation by birds. Evaported water from all tanks was replaced with creek water every 3-5 days once target salinity levels were achieved, at which time tank depth (target at 45 cm) and specific gravity were recorded, and emerged adults and floating pupae counted and removed. Water samples for nutrient analysis were taken after tank filling, and at the initiation and termination of the experimental period.

In addition to this monitoring of alkali fly production in the microcosms, benthic primary production, standing crop, and algal species composition was also measured. Primary production was estimated by measuring dissolved oxygen concentrations of the tanks over a full day-night period, using the tanks in essentially the same sense that a light-dark bottle estimate of gross photosynthesis would be made. Dawn, dusk, day and midnight readings were taken using a YSI model 58 oxygen meter, equipped with a model 5739 probe. Net daytime oxygen production was added to night respiration to determine gross photosynthetic oxygen production. Standing crop of algae was determined by extacting chlorophyll from the ungrazed algae attached to the air-lift tube from each tank (at experiment termination only). Species composition of benthic algae at different salinity levels and times will be determined from sediment surface samples taken at 1 and 2 months into the experiment (identifications by J.P. Kociolek have not been completed at this writing).

Model Development and Data Analysis

Population data from the littoral surveys was used both for establishing baseline seasonal biomass and production curves, and development of a secondary production model applied to changing conditions at varied lake levels and salinities.

Calculations

(based on model of W. Kimmerer, see his report for more detail)

Development Rate:

$$R_{i+1} = R_i e^{(-MiDi)}$$

where R_i is the rate of molting into a stage, R_{i+1} the rate of molting out of the stage, and M_i and D_i are the mortality and development time,

$$N_i = R_i\ [1-e^{(-MiDi)}]/M_i$$

where N_i is the mean number in stage i

Growth Rate:

$$w_{i+1} = w_i e^{(GiDi)}$$

where w_i and w_{i+1} are weights at beginning and end of stage i, and G_i is the growth rate,

$$W_i = w_i [e^{(GiDi)}-1]/(G_i D_i)$$

where W_i is the mean weight of the stage,

Secondary Production:

Production rate is $PR_j = {}_i(W_i N_i G_i)$,

for the time period T_j.

Production integrated over a time period:

$$IP = {}_j(PR_j DT_j)$$

where DT_j is the time between midpoints of the sampling intervals, which reduces to $(T_{j+1}-T_{j-1})/2$

Using data from laboratory experiments on the dependence of third instar growth rate and size on salinity (Herbst, unpublished), the growth term (G_i & W_i) was modified for recalculation of the model at different salinities. In addition, changes in population abundance at different lake levels due to changing areas of habitat available (substrate-dependent, assuming constant density) were used to modify the abundance term (N_i). All data were log transformed after adding 10 (lowest non-zero density typically observed) to each numerical value of density/m^2. Biomass was obtained by conversion of numerical densities according to predetermined weights for each instar. The temperature dependence of seasonal growth rates was also incorporated into the model, based on the degree-day model of Herbst (1990). Salinity effects on egg hatching success were also applied from unpublished data of T.J. Bradley.

Open water surveys of drift were analyzed to yield information on seasonal and spatial variability in density, correspondence with littoral density trends, and for comparison of average and peak densities with the foraging requirements of red-necked phalaropes.

Experiment Analysis

Statistical analysis of microcosm data involved performing analysis of variance on emergence and body size data of adult flies and pupae, comparing treatments using least significant difference tests. Descriptive statistics are also presented for data on age structure of microcosm populations, primary production rates, chlorophyll standing crop, temperature and salinity ranges of tanks, and ammonium nutrient levels.

RESULTS: Assessment Modeling and Experiments

Population Dynamics

The seasonal population dynamics for each life stage is presented in Figures 3 to 8, for the average over all 6 sample sites, for the period late April through mid-October, comparing hard and soft substrate types. The initial age structure shows that the overwintering population consists primarily of second instars and some third instar larvae. These develop into third instars, pupate and emerge as the first adult generation (Figure 9). Low numbers of overwintering adults (in reproductive diapause) produce some eggs in the spring, but most recruitment to the population comes with new adult emergence and reproduction beginning in early to mid-June. Egg production and first instar abundance decline after early August, though overall abundance in the later life stages remain high even at the final sample in October. Cooling lake temperatures after this time would effectively limit or suspend production. The population grows exponentially from May into July when carrying capacity appears to be reached. This density leveling suggests a true spatial limitation exists since otherwise an accumulation of empty and full pupa cases would occur as the growth season progresses. Removal by wave scouring may partly account for the larvae and pupae produced in excess of this carrying capacity, which would be expected to become available as drift, contributing to potential food availability (see data on open water drift densities in that section).

Comparison of substrate-specific densities for all life stages confirm that numerical abundance, or lakewide total biomass (Figure 10) were about 5-10 times higher on hard than on soft substrates. As previously observed, pupae are completely restricted to hard substrate habitat.

Population Production

Secondary production calculations for the 1991 littoral sampling data (base case of the model, Figure 10) show maximum production rates of over 100 metric tons per day, and summer standing stock biomass of about 1300 metric tons, in agreement with previous estimates (Herbst and Bradley 1992).

Preliminary model development was completed with W. Kimmerer at a late February meeting with Jones and Stokes Associates. Several components of the data base required to complete this model were not available and are in preparation by JSA. The information that is yet to be incorporated includes:

1. Revised larval growth rate data [Herbst/Kimmerer]
2. Modified substrate area curves for lake levels under consideration

a) improved resolution of the area of hard (rock) substrate found at different locations and elevations (and extending to 6410′ elevation) [this data comes from the surveys and maps of S. Stine]

b) addition of the area of vegetation zones inundated with rising lake level to account for the new habitat that becomes available as substrate for attachment of pupae and sediment stabilization [Jones and Stokes Associates, J. Jokehurst] (densities on submerged vegetation habitat are about 50% of those on rock substrate habitat, Herbst 1990, and population size should be adjusted accordingly)

c) qualitative division of soft substrate areas into zones of high density, in the vicinity of tufa/hard substrate formations, and low density, outside of these areas [After review of the data of Little et al. 1989, and Herbst and Bradley 1992, soft substrates near hard substrate formations were between 2-5 times more densely inhabited than these substrates removed from such areas. As a provisional guideline then I suggest defining the low quality soft substrates as those areas 100 horizontal meters outside the mapped hard substrate zones (of Stine), holding a density one-third that found on the soft substrates sampled during this study (which were all in areas of hard substrate).]

3. Resolve the relation used for the association between lake level and salinity [the empirical relation I have determined does not agree with the figures used by JSA]

Model comparisons to the base case are presented here for only two other lake levels - the upper and lower limits of the current substrate availability data, 6390′ and 6360′ elevation (Figures 11 and 12). At 6390′ the maximum production rate is again above 100 metric tons per day (MT/d), and biomass is projected to stand near 1400 MT. At 6360′ the maximum production rate declines to about 35 MT/d, with biomass at only 450 MT. Cumulative production in excess of the standing stock biomass level would be lost or converted in several ways: (1) mortality, (2) drift of larvae and pupae from substrates at carrying capcity, and (3) emergence of adults and conversion of benthic aquatic biomass into terrestrial shoreline adult biomass.

Open Water Drift

The drift of third instar larvae, pupae and adults from the littoral and shore regions of the lake out onto the open water surface is shown in Figures 13 and 14. Combined densities for these life stages typically average between 0 and 1 individual per cubic meter during all seasons except August, when 3 to 5 individuals/m^3 are present in the drift. This peak in potential food availability coincides with the period of excess littoral production, when densities reach carrying capacity on hard substrates. Third instar larvae are a preferred food source and occur in peak numbers both in

August and in June (Figure 14), the June larvae being derived from overwintering second instars at a time when pupae have not yet begun forming in appreciable numbers. The statistical variability of the means for each survey date are a reflection of the fact that drift, like other distribution patterns at Mono Lake, occurs in aggregated patches. These patches often correspond to foam lines or other zones of circulation convergence in the lake. Such patchiness is also apparent in a series of transect surface tows taken in late August in the NE corner of Mono Lake, through the red-necked phalarope flocking area (Figures 15 and 16). Distribution on 28 Aug shows near-shore accumulation of floating larvae, then disruption of this pattern on 29 & 30 Aug, resulting in patches composed mostly of pupae and adult flies both near shore and away from shore (intense windstorms had preceeded these samples). Average drift densities for this feeding area (10-15 ind./m^3) were greater than those observed in the open water sample surveys, showing near-shore drift (the drift source) may present an area of greater food availability to birds. Maximum numbers of total individuals were also greater for this area (50-100 indiv./m^3) than found at open water foam lines (10-20 ind./m^3). At the 1991 lake elevation of 6375′, the total surface area of the lake was 15,845 hectares (minus island areas), which when multiplied by the density per square meter of sample, yields a lakewide estimate of 10^8 to 10^9 individuals during the summer, equal to a standing biomass of about 1 MT. Seasonal trends in the open water drift further show that numbers are low in early season samples and increase as littoral densities incease, though with some lag period and a decline at the end of the season.

Microcosm Salinity Experiments

Microcosm tanks required 5 weeks to reach target salinities, during which acclimation of the inoculated benthos occurred (Figure 17), and after which the experiment was initiated. Target salinities were achieved in all but one case, where the 150 g/L tanks were actually fluctuating around a salinity of 160 g/L (Figure 18). The minimum and maximum temperatures of tanks were found to not vary significantly with salinity level (Figure 19) and so were pooled for plotting the temperature range during the entire study (Figure 20). Daytime maximum varied mostly from 22 to 28 C, and nighttime minimum from 12 to 15 C. Temperature fluctuation in the shallow littoral of the lake were in the same range for this time period.

The age structure of the microcosm population was initially composed primarily of eggs and first instar larvae (Figure 21). The area of the tank bottom was one square meter and was stocked with about 12,000 total eggs and larvae, equal to natural densities found in the lake for mixed hard and soft substrates. Second and third instars from the inoculum develop into pupae and emerge as adults during the initial emergence phase while the eggs and first instars of the inoculum have developed into a cohort of second instars (Figures 22 to 26). These ultimately mature and begin emerging as adults only in the treatment tanks at 50 g/L, at the termination of the experimental period. The other salinity treatments harbored fewer survivors, and at earlier stages of development. Some of these no doubt would have begun emerging from the tanks had the experiment been continued, but in lower numbers and later than those flies emerging from the 50 g/L treatments. Variation in emergence between tanks within each salinity treatment level is shown in Figures 27 through 31. Both the rate of emergence and cumulative numbers are significantly reduced for all steps of salinity increase (Table 1). In addition, body size (pupae and adults) becomes smaller as salinity increases (Figures 32 and 33, and Table 1).

Knowing the initial number of organisms present per area of combined sample unit (area of one cement block plus one sediment core = 82.5 cm^2), it is possible to calculate the survivorship of this cohort at the termination of the experiment by combining the average densities of all life stages remaining for one unit of both substrate sample types. Conveniently, the initial stocking density was 100 individuals/unit. Using 50 g/L as the optimum level for comparison to the higher salinities, percent survivorship at the end of the experiment and proportional effects on the rate and amount of emergence are presented as a summary of salinity effects on alkali fly production (Figure 34).

The standing crop of algae present on airlift tubes at the end of the experiment declines with increased salinity (Figure 35). These ungrazed algae were initially dominated by diatoms but by the end of the experiment had become overgrown by the filamentous alga Ctenocladus circinnatus. While this was true at 50 g/L, salinities above this level were either still in the phase of colonization by diatoms (though at reduced densities), or were nearly devoid of algae. Salinity influences both the extent and timing of algal colonization (species composition will also be examined when the data become available). Benthic primary production, as indexed by gross photosynthetic oxygen production, also shows a salinity-dependent reduction (Figure 36). The time course of dissolved oxygen change is simmilar for all treatments (Figure 37) but the magnitude of gross photosynthesis is indistinguishable among the higher salinity levels (100 to 160 g/L).

Water samples taken early in the phase of salinity adjustment (22 days) showed ammonium levels (the limiting growth nutrient in the lake, Herbst and Bradley 1989b) to vary with salinity (6-12 uM, Figure 38). Evaportive concentration of salinities in excess of the 100 g/L reference, or dilution of lower salinities would be expected to result in such a pattern. At experiment initiation, following addition of nutrient-laden sediments (day 50), ammonium levels increased in all treatments (10-20 uM). At the end of the study, ammonium levels had been depleted to levels below 2 uM in all treatments.

DISCUSSION: Assessment Interpretation

The results of the population production modeling and salinity experiments reported here reinforce earlier conclusions that declining lake levels reduce the productivity and abundance of the alkali fly population at Mono Lake. While earlier laboratory salinity tolerance studies examined physiological effects in isolation, the present studies integrate physiological with ecological effects using independent approaches - a modeling data base in which productivity is predicted based on field and laboratory measures of growth, and microcosm experiments in which production changes for the entire benthic community are directly observed.

Population data for 1991 follow the development of an overwintered cohort of larvae and the growth period of summer generations. Secondary productivity calculations using this data provide a reference lake level of 6375′ to which other designated management alternatives may be compared. This reference elevation is intermediate between 6360′ and 6390′, the lower and upper limits of data presently available on the area of benthic substrates used as habitat by the larvae and pupae of the alkali fly (data used to generate model predictions). The preliminary results of the modeling shows lakewide aquatic biomass of 1400 metric tons at 6390′, 1300 at 6375′, and 450 at 6360′. More than 50% of the biomass produced currently is lost over this last 15 foot drop in lake level, due primarily to loss of hard substrate habitat, but little change in production occurs between 6375′ and 6390′. These results are consistent with the habitat-based model predictions of Herbst and Bradley (1992). Though the population data presented here provide a useful baseline for future comparisons, further examination of lake level alternatives requires the model revisions outlined in results.

The area of hard and soft substrate types available as habitat at different lake levels is an important component of the modeling procedures that have been developed for the alkali fly at Mono Lake. An assumption of these models has been that substrate is limiting to population size and that during the season of production, for any lake level, substrates are inhabited at a constant density. Hard substrates (primarily tufa) harbor the greatest numbers, and availability of this habitat is a regulator of population size. The alternate view, that population size does not change as lake levels fluctuate, would posit a model that assumes constant population size rather than constant density. These alternatives are testable by monitoring substrate-specific densities at different lake levels. If population size is constant, densities should increase as lake level declines, and decrease as the lake level rises. Under the current range of lake levels where hard substrate area is most changeable, such an assumption could be most easily tested with a yearly monitoring program.

Substrate surveys conducted for the population analysis presented here support the assumption of constant density since hard substrate densities, after an initial colonization phase, do reach a constant limiting level during the period of summer productivity. Basic resource-limitation considerations would also argue that such an assumption is most likely because of finite space and food availability. Constant density may actually be a conservative assumption since it is likely that carrying capacity may decline at lower lake levels due to decreased production of algal food at elevated salinity, and lower quality hard substrate types (pumice and gaylussite substrate in deep water currently, would present an inferior surface for colonization compared to tufa).

Dislodgement of larvae and pupae from littoral benthic habitat is ultimately the source for drift of these stages out into open water. For the surveys conducted here this results in a steady-state of about 1 metric ton floating on the lake during most of the summer, and somewhat more in August. Some equilibrium is implied between the generation of this drift and its deposition as onshore windrows or consumption by avian predators. Little or no drift exists in seasons when littoral production is not occuring (early season samples here).

Mechanisms that concentrate alkali fly drift or any other food source are important to facilitating foraging by birds. Surface foam lines that form at zones of convergence of lake currents serve to cocentrate food. Phalaropes and gulls were observed feeding in such areas, especially early in the season when open waters densities of larvae and pupae were low. Windrows of pupae cast upon the shore also concentrate this food, but desiccation and decomposition may often compromise nutritional quality. Long-shore pools protected by sand berms (along the eastern shores) may collect large numbers of drifting larvae and pupae, attracting shorebirds. Adult flies aggregating on shores around much of the perimeter of the lake are focal points for feeding by many shorebirds. Though larvae and pupae clearly become aggregated on tufa substrates, there are apparently no birds able to take advantage of this submerged food source.

The highest densities observed in drift samples in open water (at foam lines) were 10-20 individuals/m^3, and 50-100 ind./m^3 in the NE lake region used by red-necked phalaropes as a feeding area. Though phalaropes forage where food is most available, even these observed maximum local densities are 5 to 10 times lower than the density at which feeding success drops significantly relative to conditions where food is more available (M.Rubega, personal comm.).

Since foraging efficiency of these phalaropes under natural conditions at Mono Lake are sub-optimal, questions about the continued ability of the birds to use the lake become how far must the birds range, or how much time must they spend to obtain sufficient food to (a) maintain a minimum body weight, or (b) grow and store fat for molting/migration. Though we do not know precisely how the declining benthic productivity with lower lake levels would affect birds at Mono Lake, one approach would be to assume that food availability (as drift) scales to the abundance of the source (littoral) population, corrected for the changing lake surface area:

$$[\text{Drift Density}]_{\text{level x}} = [B_{\text{level x}}/B_{\text{level 6375}}]*D_{6375} \;/\; [A_x/A_{6375}]$$

(ind./m^3)

where B = lakewide standing stock biomass
D = drift density at the reference lake level
A = surface area of the lake (at level x and reference level)

Using projections of the present production model, at a lake level of 6390′, food density availability would be reduced to 88% of that present at 6375′ due to the larger area of the lake surface that food would be spread over. At 6360′, availability would be reduced to 43% that available at the reference level, even though the surface area is smaller. At this lower elevation, the foraging area and/or time requirements would have to more than double in order to maintain the reference level of either body weight or fat storage. Time and energy budgets for these birds are needed to determine the extent to which such behavioral/metabolic response is possible. Refer to the technical report prepared by M. Rubega for further treatment of this and subject and related information.

The microcosm experiments provide a clear demonstration that salinity regulates benthic productivity. Alkali fly production was optimum at 50 g/L and was reduced in approximate proportion to salinity increase in the other treatments (Figure 34). Productivity of tanks at the current salinity of 100 g/L was less than half that observed at the pre-diversion salinity of 50 g/L, and was negligable at the highest salinity (160 g/L). Survivorship was also reduced by about 15% for each step of salinity increase, down to only 30% surviving in 160 g/L relative to 50 g/L.

These results provide independent validation of the production model predictions, even though substrate area limitation was not taken into account in the microcosms. The extent of this salinity effect on production argues that the physiological effects of salinity on larval growth that were used in the model underestimate salinity limitations extending to the population level.

Salinity constraints on life history traits such as body size were also observed in the microcosms, consistent with previous laboratory data. Adult and pupa body size decline with salinity increase (Table 1). As the body size of pupae become smaller, a greater proportion of these will fail to emerge as adults, and those adults that do emerge have a decreased chance of surviving or reproducing (Herbst, 1986). Adults from the second emergence phase observed in tanks at 50 g/L were noted to be unusually large and robust flies. Having spent virtually their entire life span in this salinity (from eggs or first instars), they are a better indicator of the full effects of salinity on growth. Salinity not only limits productivity, but delays development such that later emergence of fewer (and smaller?) survivors would occur from the other tank treatments. Experiments should be repeated for a longer period to measure the effect on production over a full life cycle for all treatments. Whether adult females discriminate by salinity prior to entering water to feed or lay eggs should also be examined to determine if there may be behavioral constraints on habitat use.

In addition to reductions in alkali fly production, salinity limitations on algal production were also observed. Laboratory studies of algal cultures have previously demonstrated such an effect (Herbst 1986, Herbst and Bradley 1989b). Reduced primary production and changes in algal species composition of the microcosms were probably an important component of the salinity effect on alkali fly production, limiting growth due to decreased algal food availability and quality.

Nutrient ammonium levels of the microcosms were established in the same range as occur naturally in Mono Lake (11 uM, Dana/Heil pers. com.) and subsequently vary in proportion to the degree of salinity concentration applied to each treatment. Though this introduces a confounding chemical variable to the experiment, it actually reinforces the conclusion that salinity is the primary regulator of productivity because the nutrient gradient here would have stimulated the opposite effect on production. Ammonium levels are well below the concentration where any toxic effect would occur. Ammonium is depleted to low levels in all treatments by the end of the experiment, raising the question of how it is lost if there is only limited algal uptake at the higher salinities. Loss to the atmosphere by salinity-dependent degassing is one possibility that deserves greater attention since it could have an important bearing on the nutrient budget of a fluctuating Mono Lake.

In conclusion, the compounded effects of salinity observed in experimental microcosms on the alkali fly and its associated ecological community result in more pronounced limits on production than would be predicted by physiological studies alone. With revision of the production model it will be possible to compare the microcosm results with independent production predictions based both on physiological salinity limitations and ecological habitat availability (substrate) limitations.

The development of management guidelines for Mono Lake need to balance ecological values against economic and societal values. Using production as an indication of ecological value, the present studies show that the pre-diversion salinity of 50 g/L is optimum and that on the order of half this ecological value has been lost with lake decline to present conditions. Recovery of this value is possible since the capacity for production to respond given conditions of lower salinity and increased habitat availability has not been impaired.

Acknowledgements

First and foremost I thank Mike Embury who assisted me throughout this project and was integral to devising plans, trouble shooting, and laboring long hours under the sun and in the lab. Dan Dawson and Scott Roripaugh of SNARL provided a water pump and help in initial filling of tanks. S. Hurlbert and J. Melack offered useful experimental design suggestions and discussion. G. Dana and D. Heil crewed the boat and helped with open water surveys. C. Milliron helped transport equipment and conduct surveys. R. Puskar set up and maintained the solar-powered aeration system. W. Kimmerer collaborated in development of the population production model. Algal taxonomic identifications were provided by J.P. Kociolek of the California Academy of Sciences. M. Rubega and C. Elphick helped conduct open water transects in the phalarope flocking area. Habitat area and substrate mapping was completed by S. Stine. J. Bischoff and T. Bradley were important sources of data and insight.

Funding support and helpful guidance were provided by the Los Angeles Department of Water and Power (K. Covert, B. White), the State Water Resources Control Board (J. Canaday and S. Herrera), and Jones and Stokes Associates (R. Brown and T. Beedy).

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TABLE 1. **Statistical Summary of Salinity Comparisons from Experimental Microcosms**

Least significant difference tests following ANOVA [salinity levels not joined by common underline are different at the .05 level]

Body Size Comparisons (also see related figures) arranged in order of decreasing size:

Adult Flies	$\underline{50 \quad 75} > \underline{100 \quad 125}$
Pupae (empty) sample #1	$\underline{50 \quad 75 \quad 100} > \underline{125}$
Pupae (full) sample #1	$\underline{50 \quad 75 \quad 100} > \underline{125 \quad 160}$ $\underline{} >$
Pupae (empty) sample #2	$\underline{50} > \underline{75 \quad 125 \quad 100}$
Pupae (full) sample #2	$\underline{50} > \underline{75} > \underline{100 \quad 125 \quad 160}$

Adult Emergence Comparisons: (see related figure)

Slope of initial emergence phase
(=flies/day production rate)
calculated from day 10 to 32 for 50/75 g/L
and from day 10 to 40 for 100/125/160 g/L:

$\underline{50} > \underline{75} > \underline{100} > \underline{125} > \underline{160}$

Cumulative adult emergence at completion of initial phase of emergence (plateau, day 47):

$\underline{50} > \underline{75} > \underline{100} > \underline{125} > \underline{160}$

Cumulative adult emergence at termination of the experiment (final sample, day 67):

$\underline{50} > \underline{75} > \underline{100 \quad 125} > \underline{160}$

Figure Legends

Figure 1. Map of Mono Lake showing locations of littoral sample sites, open water sample stations, and transects in the phalarope feeding area.

Figure 2. Array of tanks for microcosm salinity experiment. Loacated 100 meters from shore of Mono Lake near DWP boat dock. Symbols: PV = photovoltaic panels, 12V = deep cycle storage batteries, Aer. = aeration pump and air lines. Treatments were arrayed such that none were repeated in any row or column.

Figure 3. Seasonal abundance of eggs on hard and soft substrate types averaged over littoral benthic sampling sites for 1991.

Figure 4. Seasonal abundance of first instar larvae on hard and soft substrate types averaged over littoral benthic sampling sites for 1991.

Figure 5. Seasonal abundance of second instar larvae on hard and soft substrate types averaged over littoral benthic sampling sites for 1991.

Figure 6. Seasonal abundance of third instar larvae on hard and soft substrate types averaged over littoral benthic sampling sites for 1991.

Figure 7. Seasonal abundance of full pupae (developing or failed) on hard and soft substrate types averaged over littoral benthic sampling sites for 1991.

Figure 8. Seasonal abundance of empty pupae (adults emerged) on hard and soft substrate types averaged over littoral benthic sampling sites for 1991.

Figure 9. Seasonal abundance index of adult alkali flies along shores of littoral sampling sites for 1991.

Figure 10. Population production model: Base case elevation 6375'.

Figure 11. Population production model: elevation 6390'.

Figure 12. Population production model: elevation 6360'.

Figure 13. Open water drift of third instar larvae, pupae (full) and adults averaged over 10 sampling stations. Units in thousands per 100 cubic meters of sample.

Figure 14. Open water drift of third instar larvae only, averaged over 10 sampling stations. Units in individuals per 100 cubic meters of sample.

Figure 15. Open water drift transects through phalarope feeding area for larvae, pupae and adults per cubic meter.

Figure 16. Open water drift transects through phalarope feeding area for third instar larvae per cubic meter.

Figure 17. Time course of salinity adjustment in experimental microcosm tanks. Filling on June 20 (day 0), inoculation on day 20 and day 45 (just prior to experiment initiation). 171 190= July 9

215 = Aug 3

Figure 18. Range of salinities achieved during experimental period and comparison to target salinities.

Figure 19. Temperature range in microcosms are not significantly different over the salinity treatment levels.

Figure 20. Time course of temperature range in microcosms.

Figure 21. Age structure of inoculum population for all microcosm tanks. Number expected /sample unit (cement block + sediment core).

250 Sept 7

Figure 22. Population age structure on sediment cores from the first sample date (day 80). Sample size = 40 (10 cores from each of 4 tank replicates). Standard errors less than 3 for all data ranges and usually much lower.

Figure 23. Population age structure on cement blocks from the first sample date (day 80). Sample size = 40 (10 blocks from each of 4 tank replicates). Standard errors less than 3 for all data ranges and usually much lower.

282 ~~Sept 29~~ Oct 9

Figure 24. Population age structure on sediment cores from the second sample date (day 112). Sample size = 40 (10 cores from each of 4 tank replicates). Standard errors less than 3 for all data ranges and usually much lower.

Figure 25. Population age structure on cement blocks from the second sample date (day 112). Sample size = 40 (10 blocks from each of 4 tank replicates). Standard errors less than 3 for all data ranges and usually much lower.

Figure 26. Cumulative adult emergence curves during experimental period (mean of 4 microcosm tanks each).

Figure 27. Variability in adult emergence by treatment (50 g/L).

Figure 28. Variability in adult emergence by treatment (75 g/L).

Figure 29. Variability in adult emergence by treatment (100 g/L).

Figure 30. Variability in adult emergence by treatment (125 g/L).

Figure 31. Variability in adult emergence by treatment (160 g/L).

Figure 32. Summary of salnity effects on production terms in microcosm experiments relative to 50 g/L optimum.

Figure 33. Reduction in adult body size with salinity in microcosm experiments. The few adult flies emerging from 160 g/L are excluded from the analysis of body size because most emerged early (<2 weeks) and are not representative of flies exposed to the experimental treatment, being derived from third instar larvae pupating within no more than a few days of being introduced into the tanks.

Figure 34. Pupa body size from cement blocks at (A) sample date #1 (day 80) and (B) sample date #2 (day 112). Adults have emerged from empty pupae while full pupae are some mixture of developing and failed adults (the full pupae are smaller because a higher proportion have failed). No empty pupae occurred in samples at 160 g/L. Means of 4 replicate tanks/treatment.

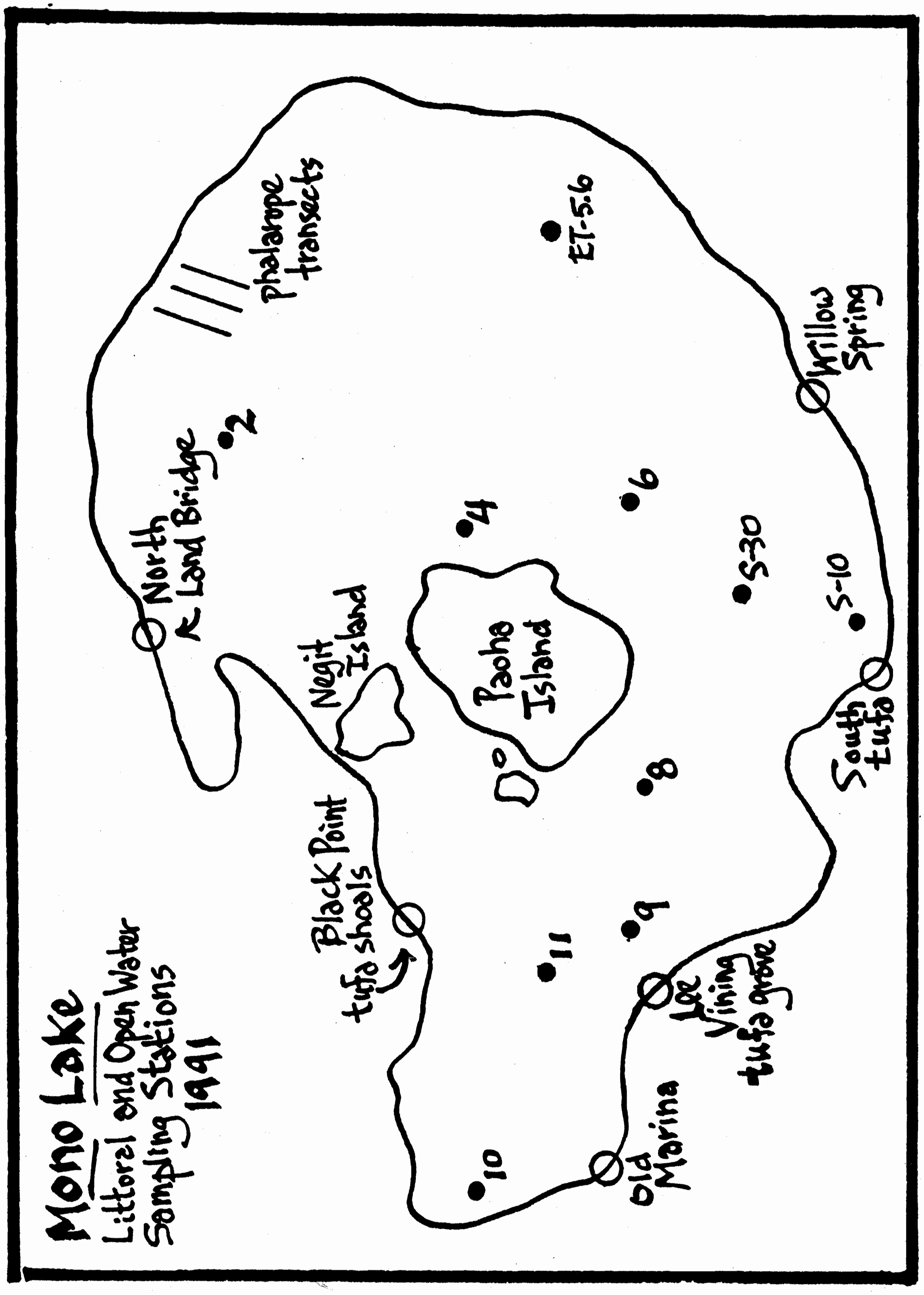
Figure 35. Standing crop of algae (as chlorophyll a) on an ungrazed sample surface (airlift tubes) from experimental microcosms.

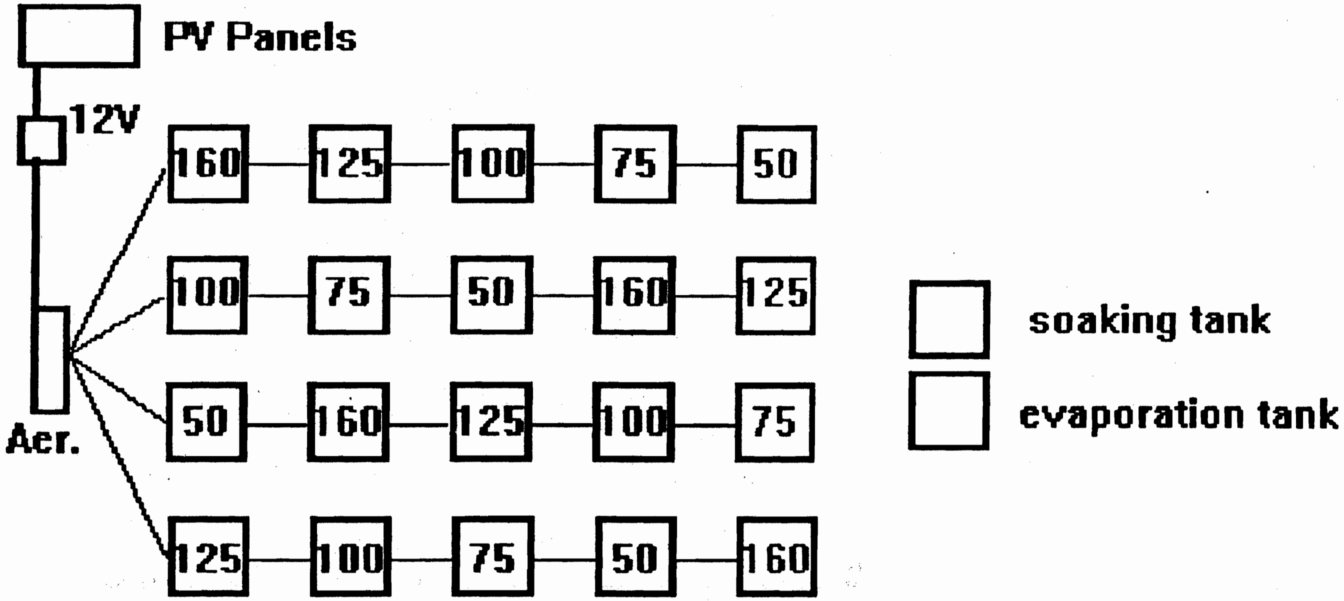
Figure 36. Benthic primary production of microcosms as gross photosynthetic oxygen production over a full day-night cycle.

Figure 37. Time course of tank metabolism during net daytime oxygen production and nighttime respiration.

Figure 38. Ammonium concentration at different phases of the microcosm experiment (mean of 4 tanks/treatment and standard deviation)

Figure 1


Mono Lake
Littoral and Open Water Sampling Stations 1991
phalarope transects
ET-5.6
Willow Spring
2
North Land Bridge
4
6
S-30
S-10
Negit Island
Paoha Island
South tufa
8
Black Point tufa shoals
9
11
Lee Vining tufa grove
10
Old Marina

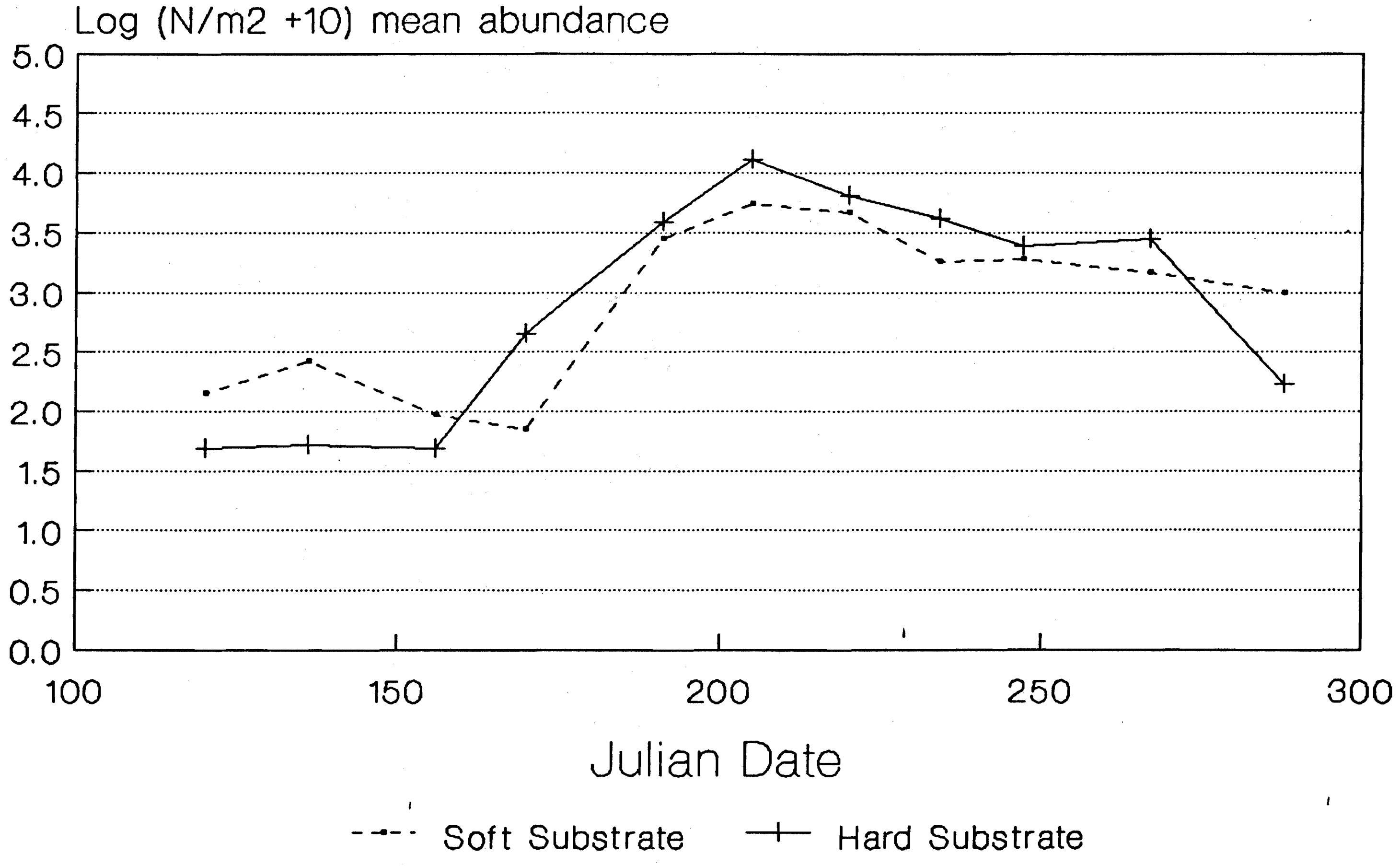


MICROCOSM TANK ARRAY

Figure 2

Alkali Fly Egg Densities

season and substrate

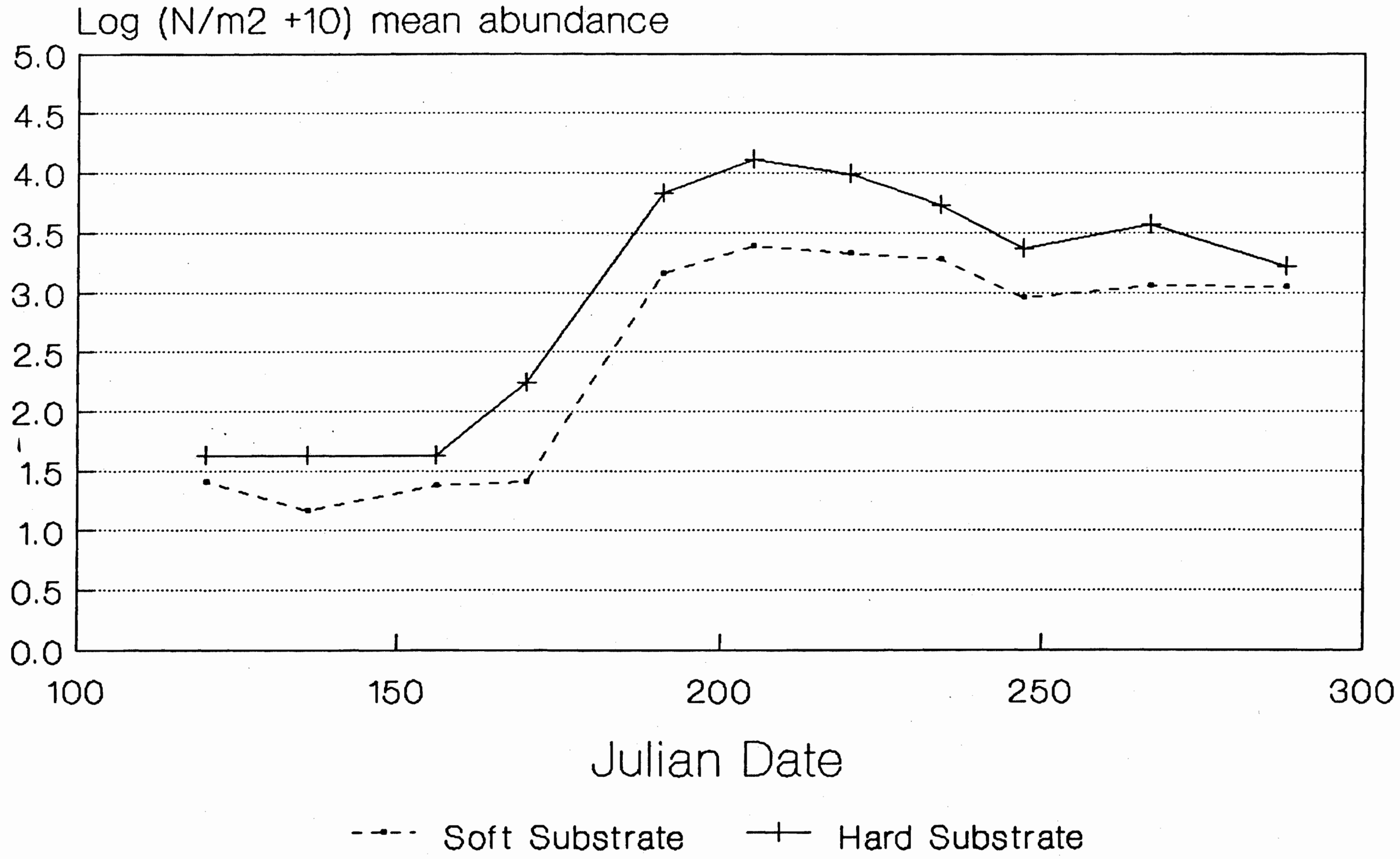


end of April to middle October

Figure 3

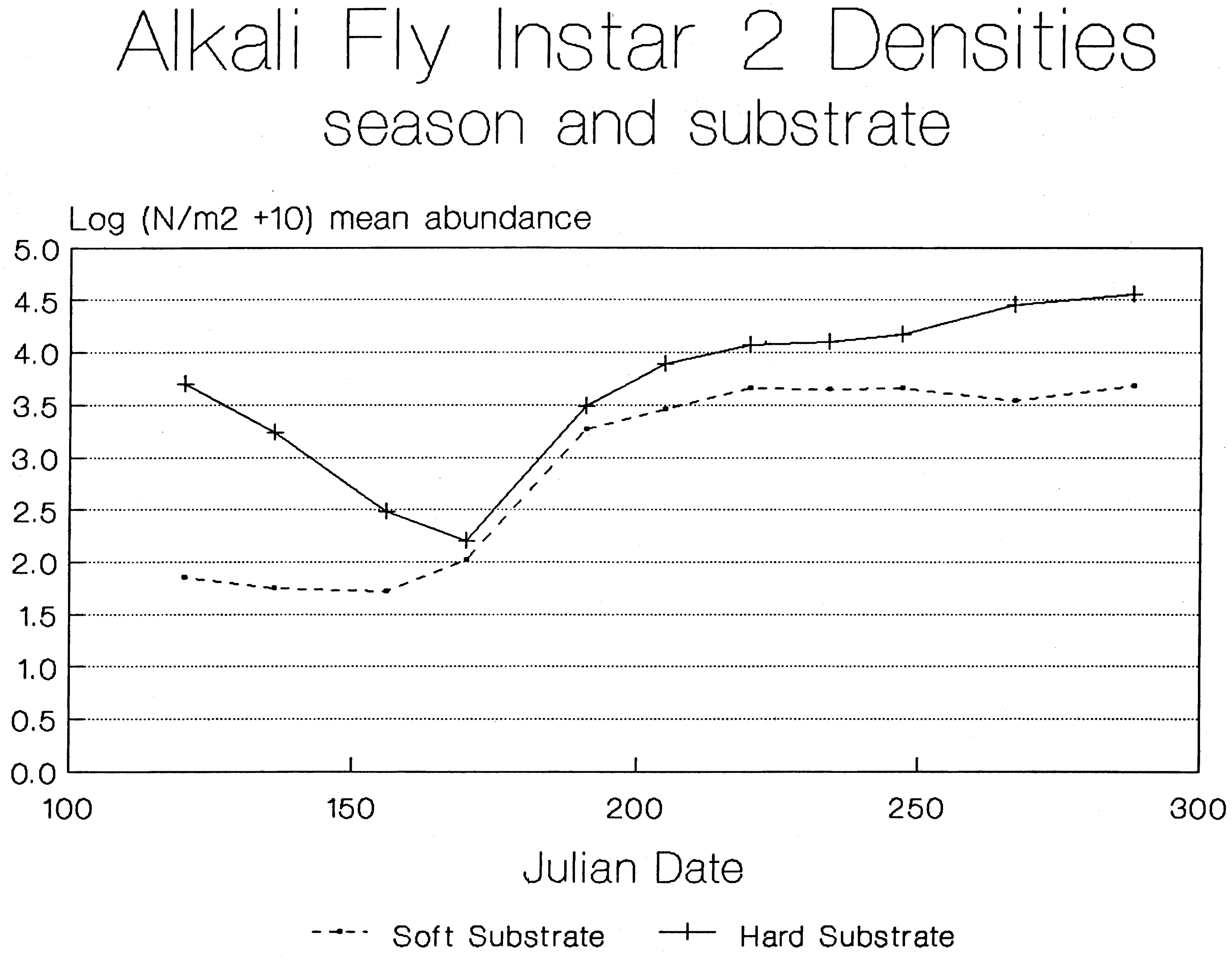
Alkali Fly Instar 1 Densities

season and substrate



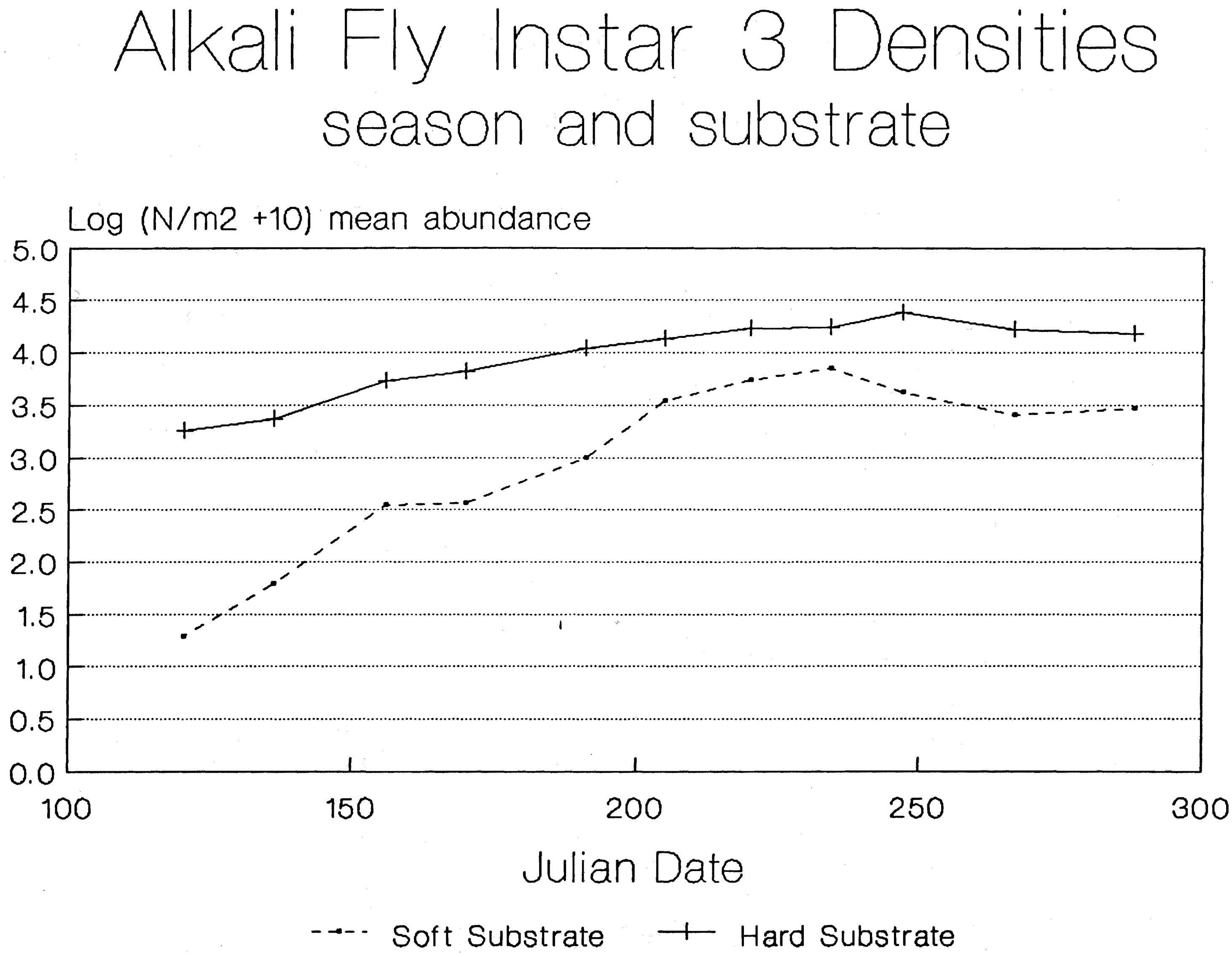
end of April to middle October

Figure 4



end of April to middle October

Figure 5

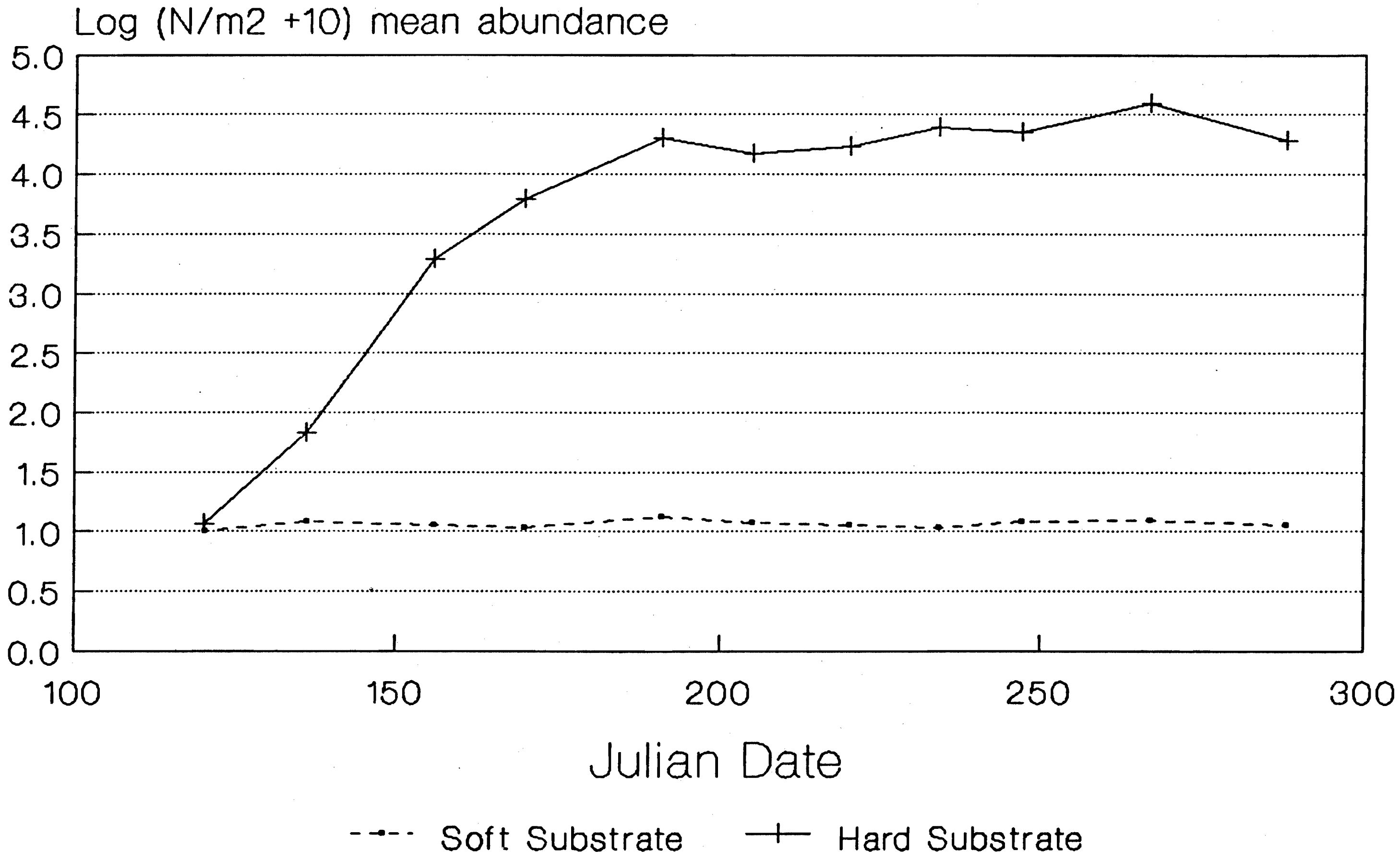


end of April to middle October

Figure 6

Alkali Fly Pupae/Full Densities

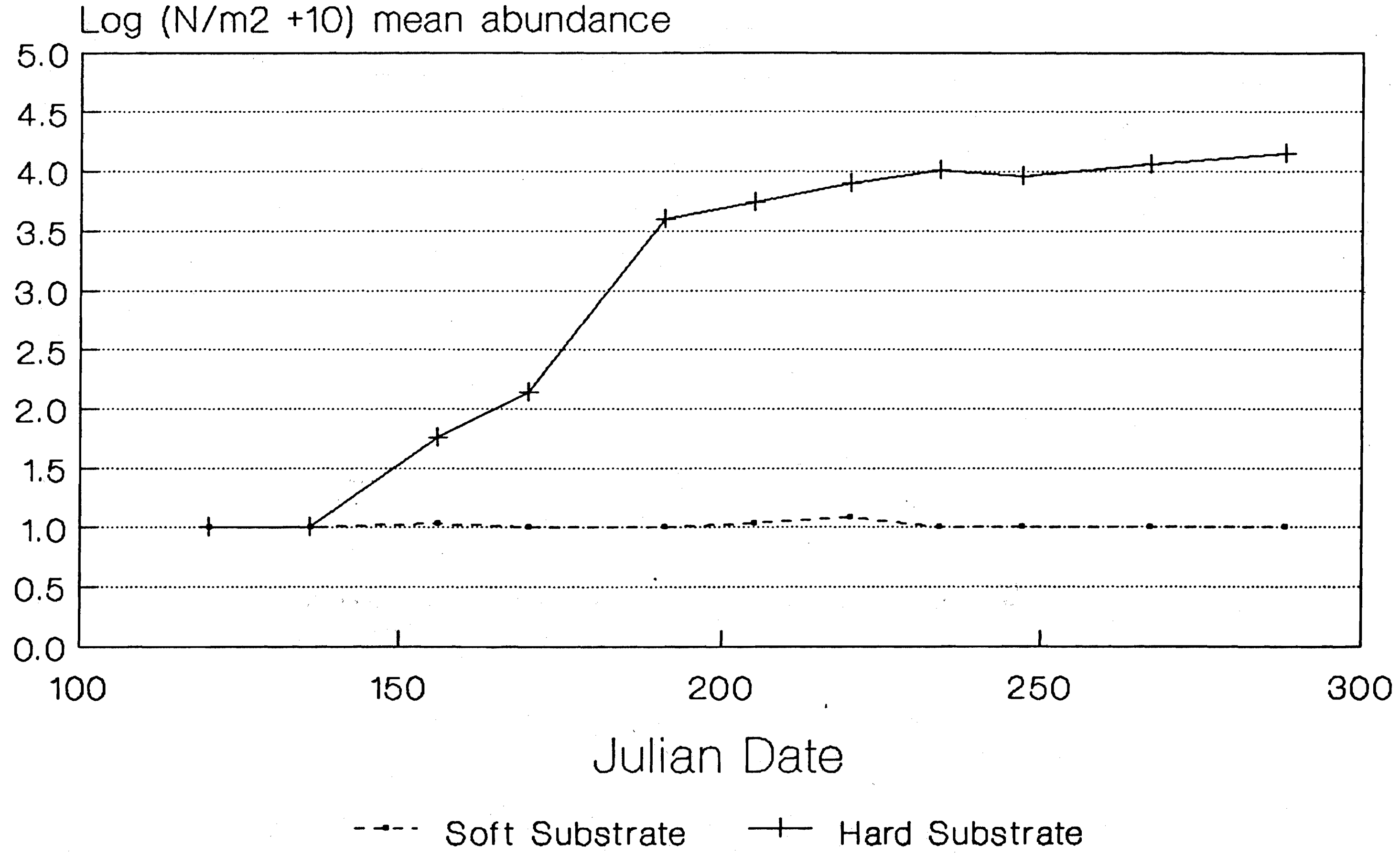
season and substrate



end of April to middle October

Figure 7

Alkali Fly Pupae/Empty Densities
season and substrate



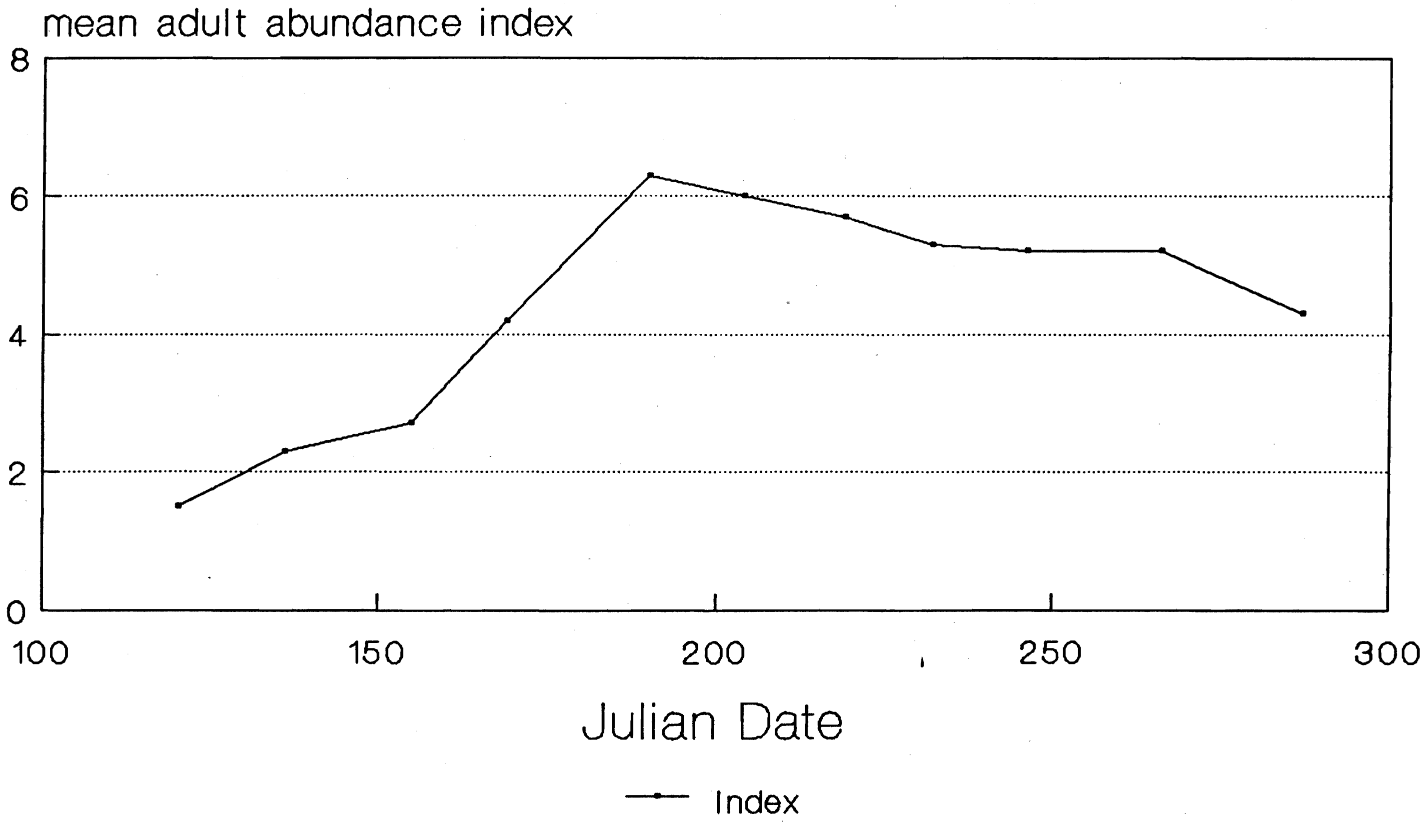
end of April to middle October

Figure 8

Figure 9

Adult Abundance Index

seasonal averages



index based on product of observed dispersion (local=1;widespread=2), and frequency (rare=1;common=2;abundant=3)

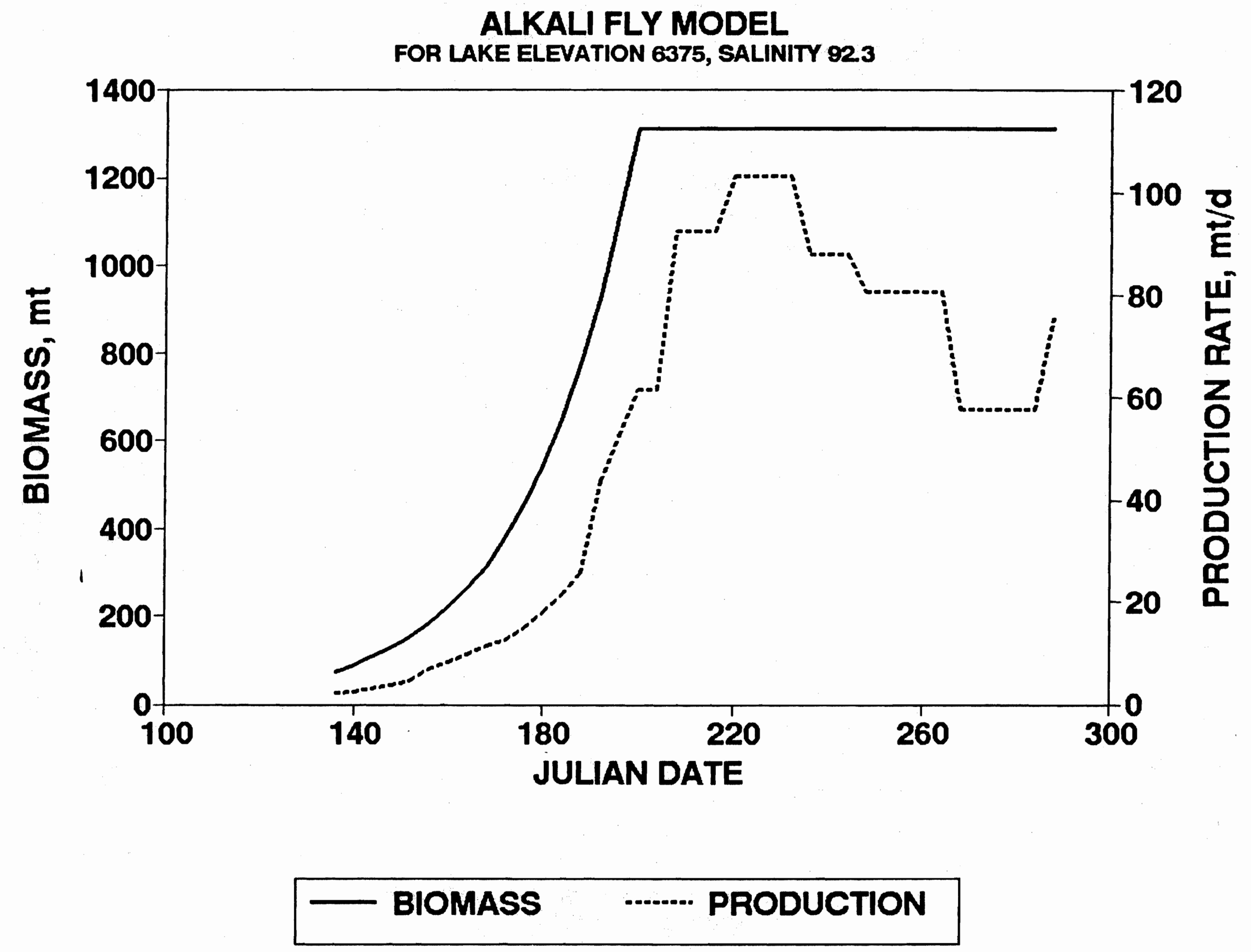

ALKALI FLY MODEL
FOR LAKE ELEVATION 6375, SALINITY 92.3
BIOMASS, mt
0
200
400
600
800
1000
1200
1400
PRODUCTION RATE, mt/d
0
20
40
60
80
100
120
100
140
180
220
260
300
JULIAN DATE
BIOMASS
PRODUCTION

Figure 10

ALKALI FLY MODEL

FOR LAKE ELEVATION 6390, SALINITY 71.2

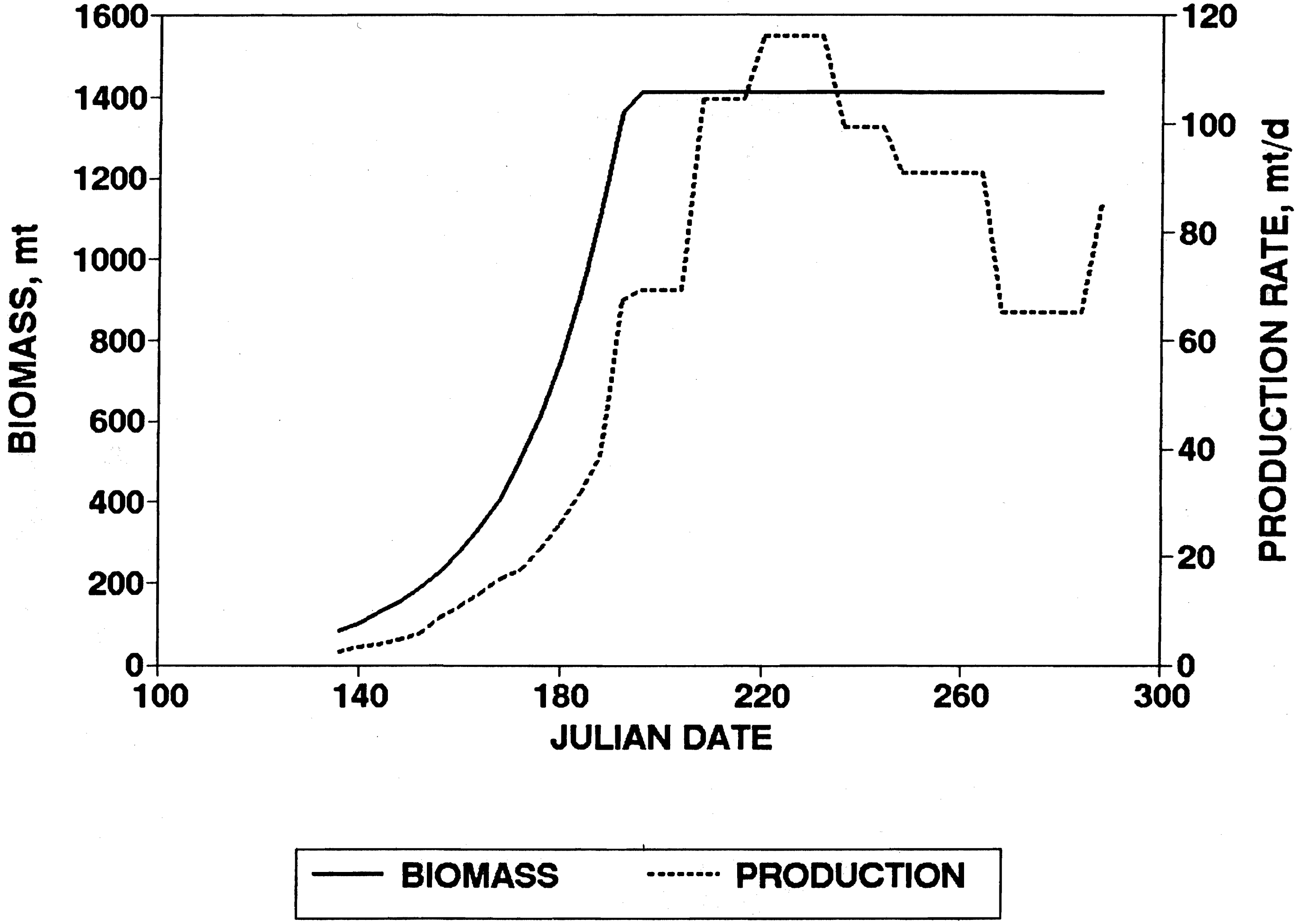


Figure 11

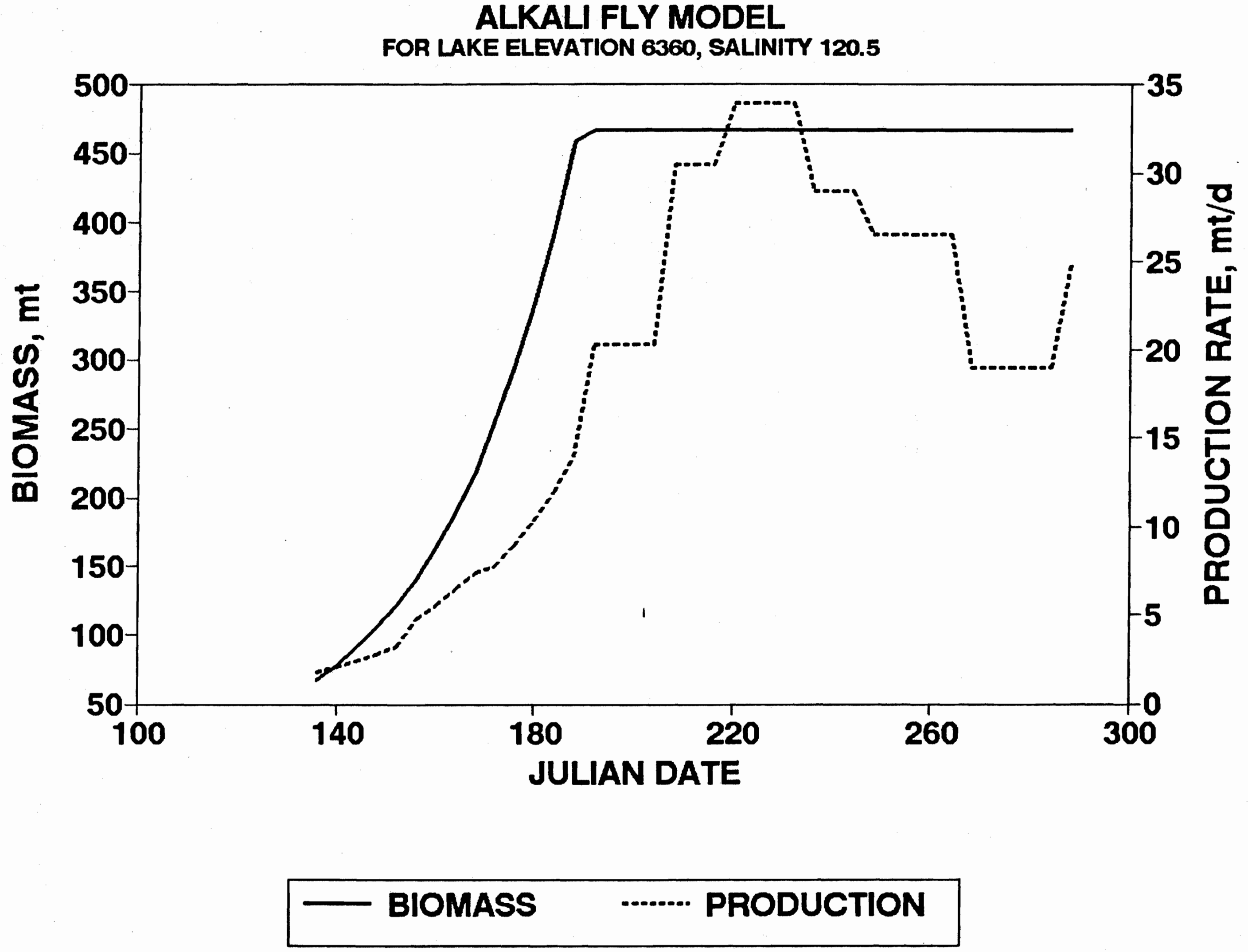
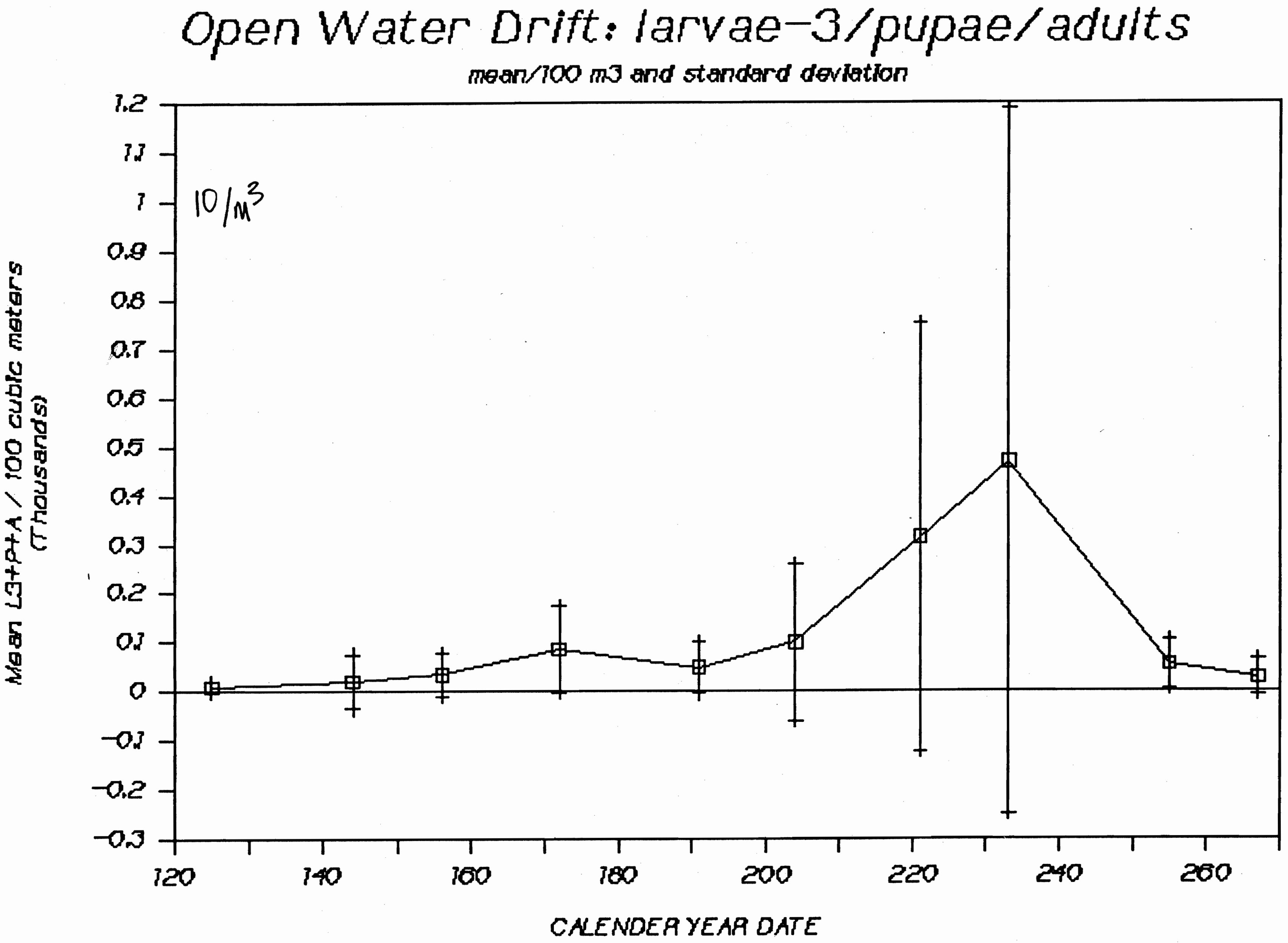

ALKALI FLY MODEL
FOR LAKE ELEVATION 6360, SALINITY 120.5
BIOMASS, mt
500
450
400
350
300
250
200
150
100
50
PRODUCTION RATE, mt/d
35
30
25
20
15
10
5
0
100
140
180
220
260
300
JULIAN DATE
BIOMASS
PRODUCTION

Figure 12



Open Water Drift: larvae-3/pupae/adults
mean/100 m3 and standard deviation
10/m³
Mean L3+P+A / 100 cubic meters (Thousands)
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
-0.2
-0.3
120
140
160
180
200
220
240
260
CALENDER YEAR DATE

Figure 13

show
points, not ±SD

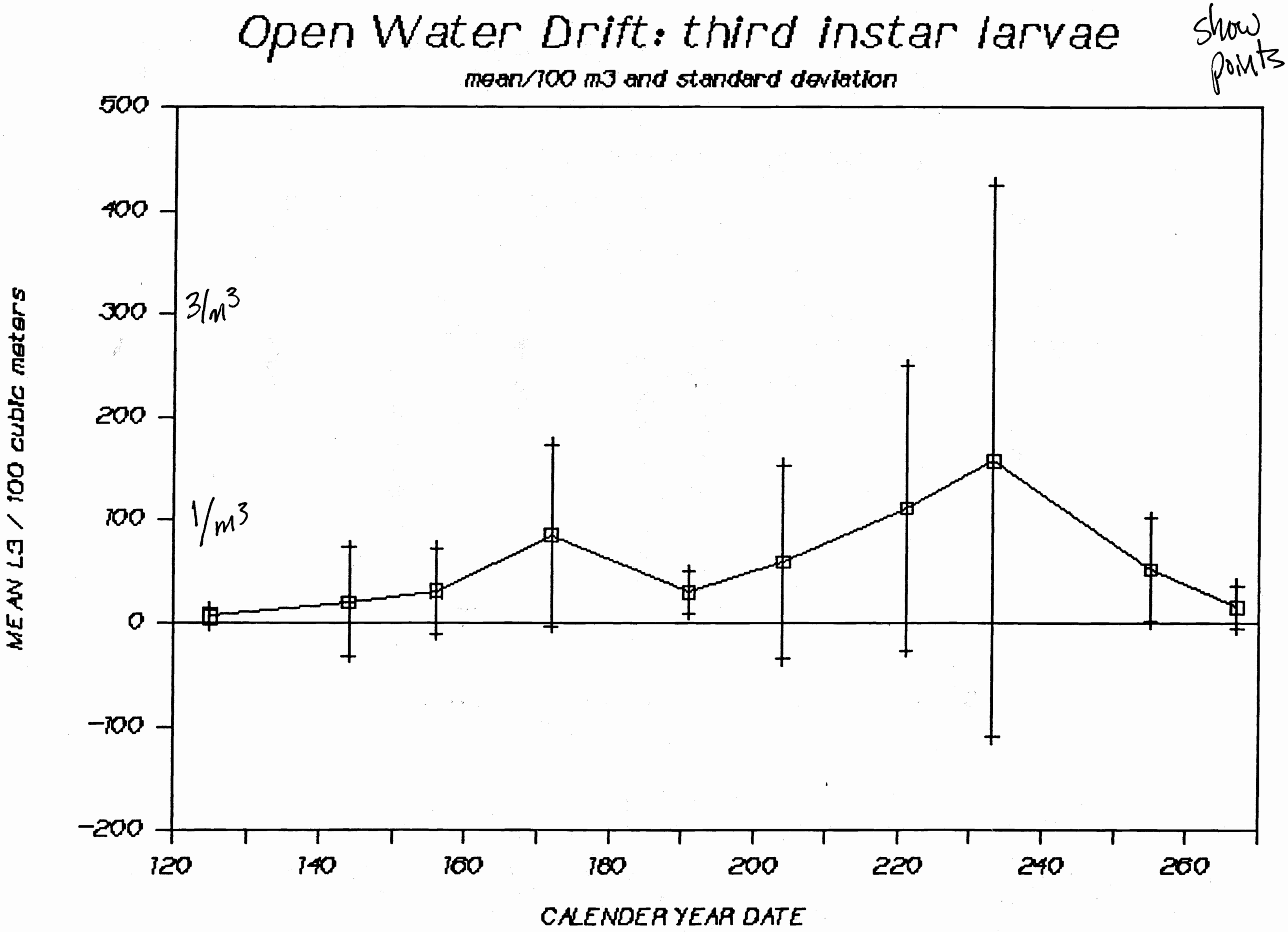
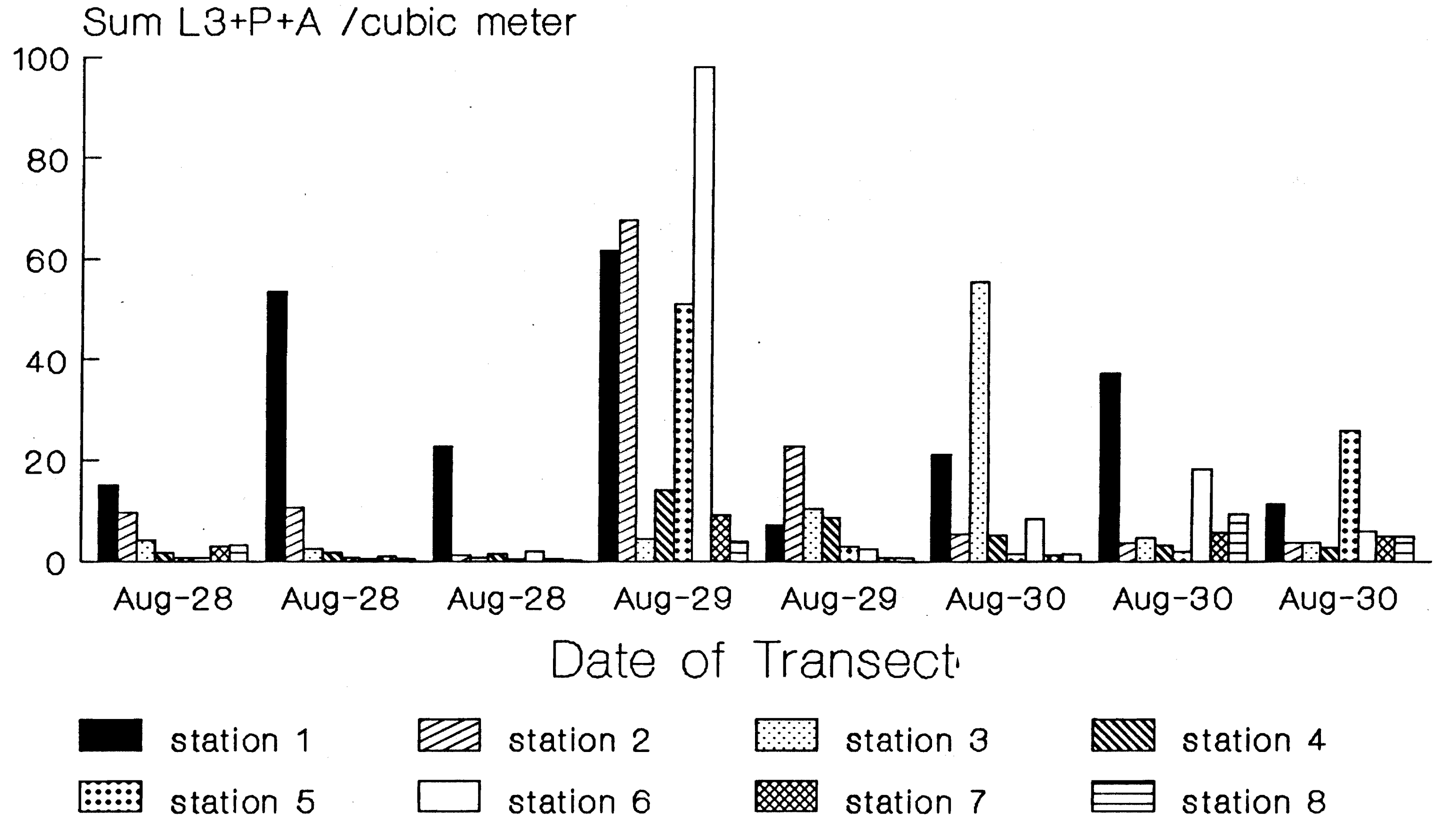


Figure 14

Open Water Drift Transects

total larvae+pupae+adults /cubic meter

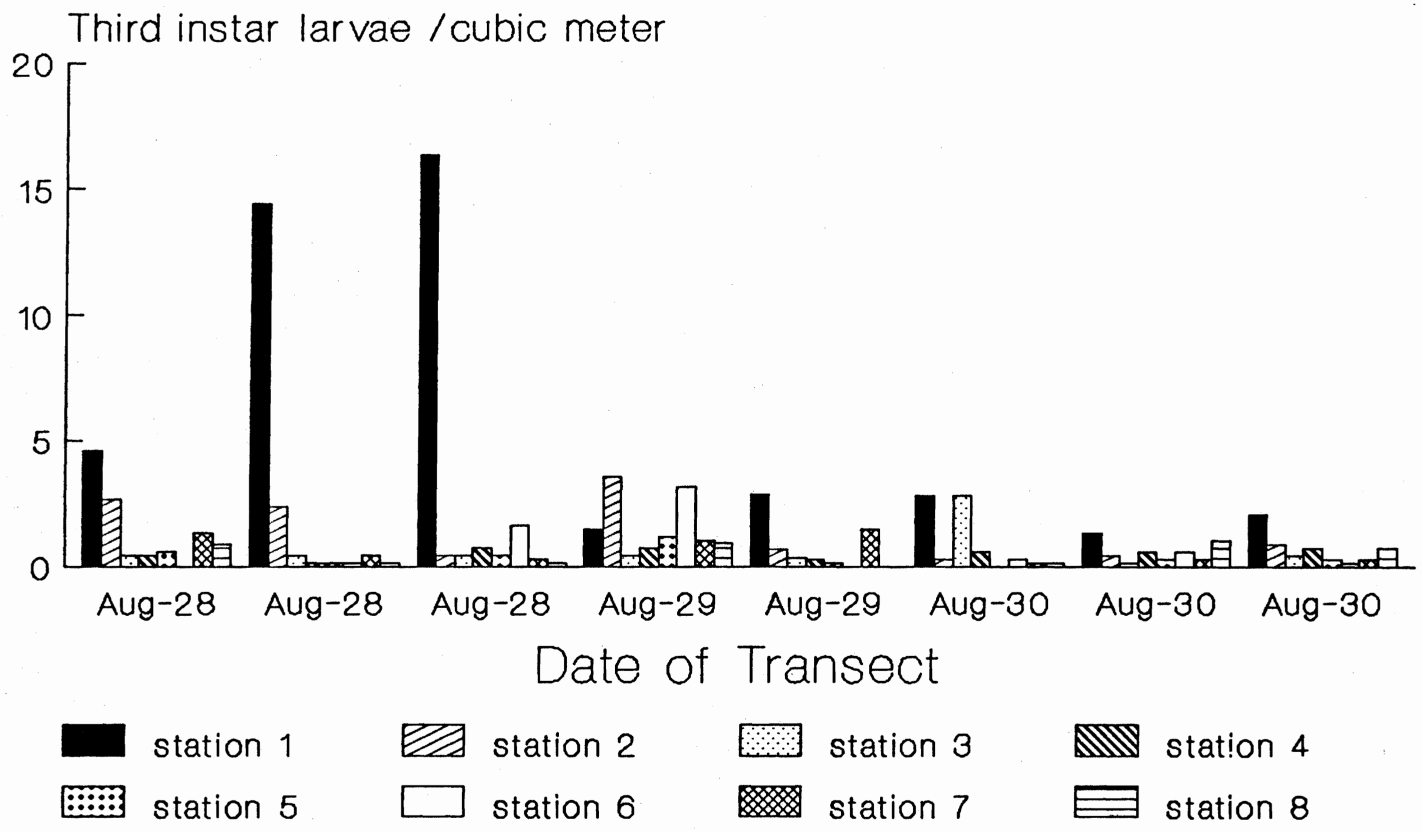


transects extend from shore to open lake
NE Mono Lake RN phalarope feeding area
(stations 1-4 within area, 5-8 outside)

Figure 15

Open Water Drift Transects

third instar larvae /cubic meter



transects extend from shore to open lake
NE Mono Lake RN phalarope feeding area
(stations 1-4 within area, 5-8 outside)

Figure 16

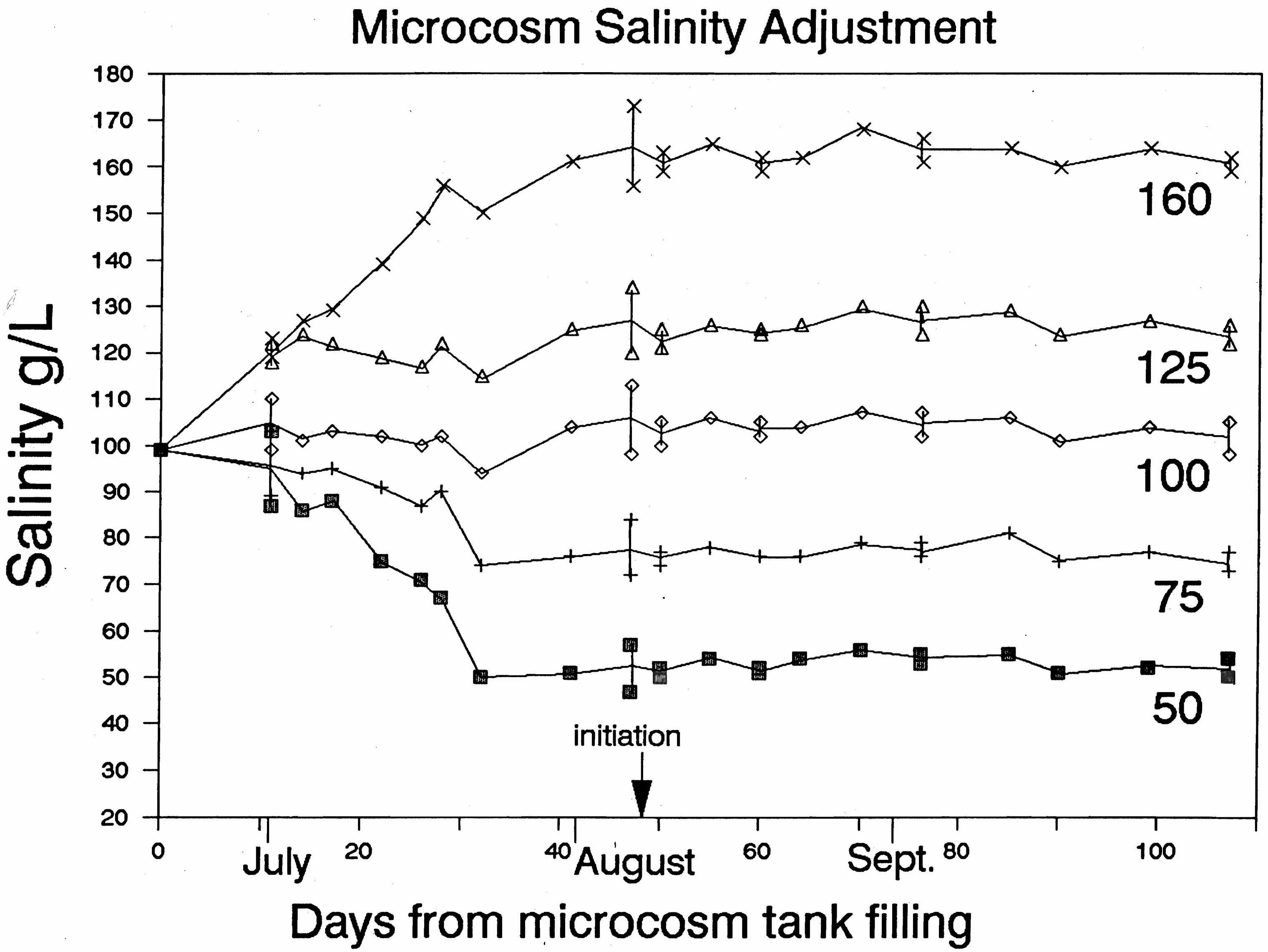

Microcosm Salinity Adjustment
Salinity g/L
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
20
160
125
100
75
50
initiation
0
20
40
60
80
100
July
August
Sept.
Days from microcosm tank filling

Figure 17

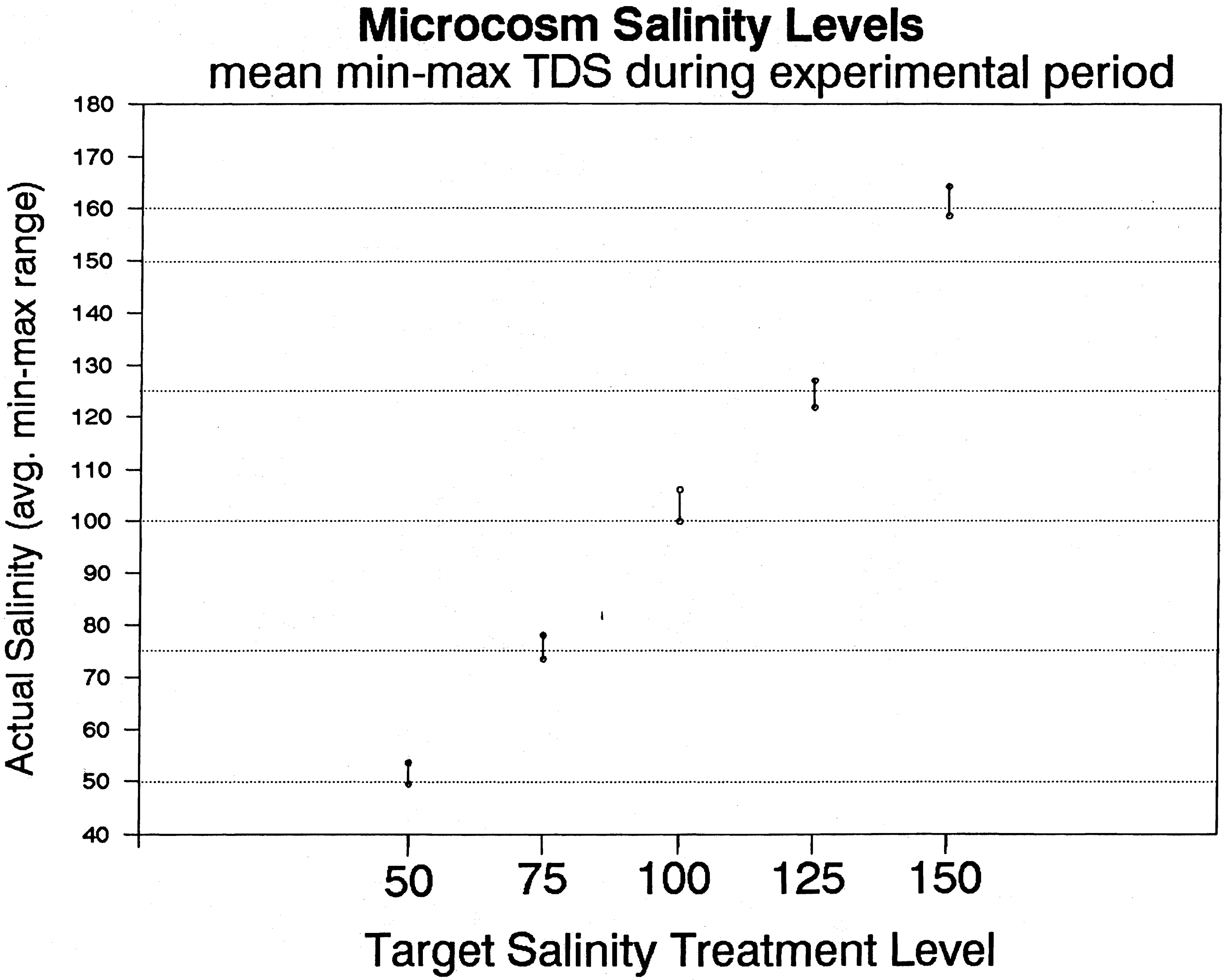
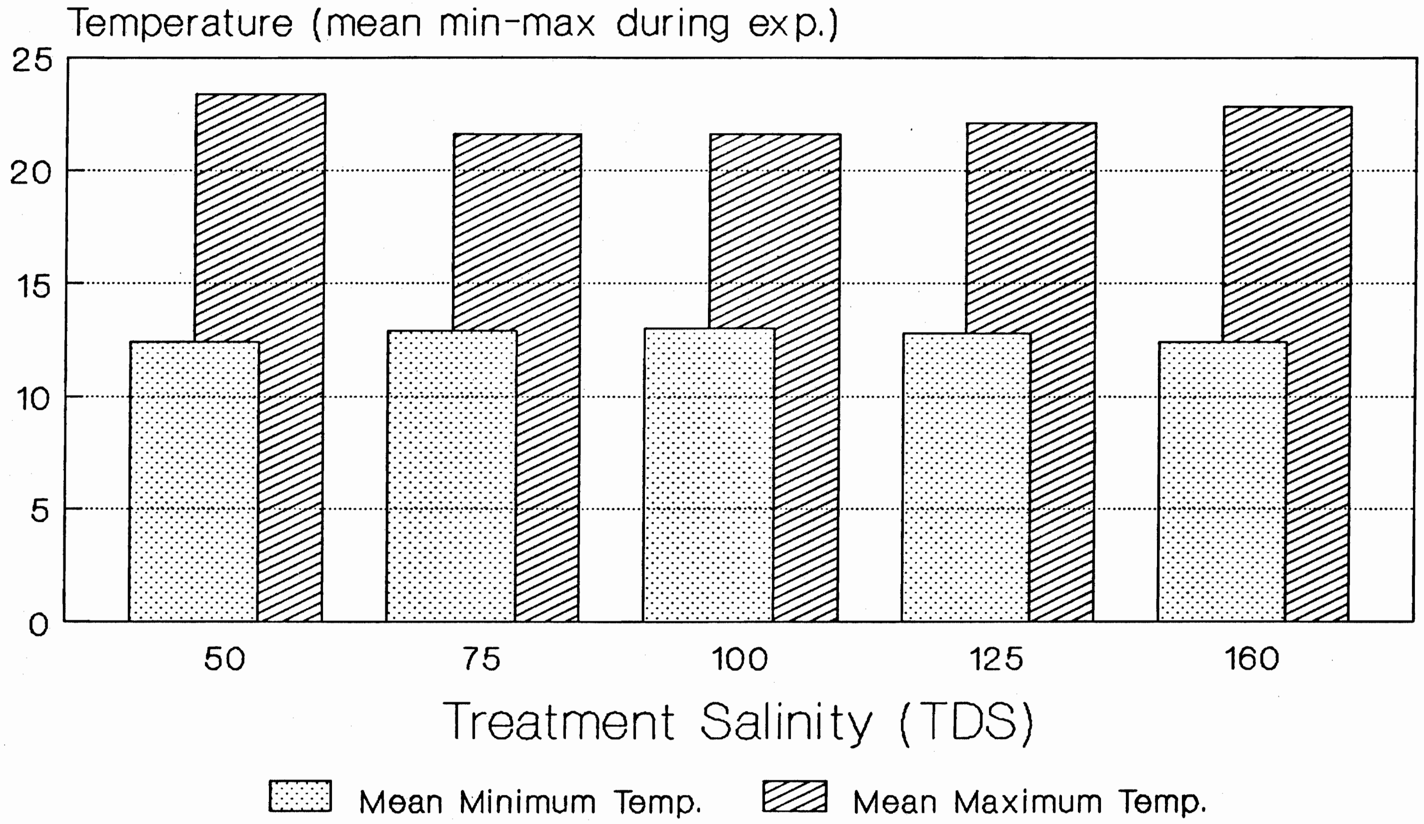

Microcosm Salinity Levels
mean min-max TDS during experimental period
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
Actual Salinity (avg. min-max range)
50
75
100
125
150
Target Salinity Treatment Level

Figure 1B

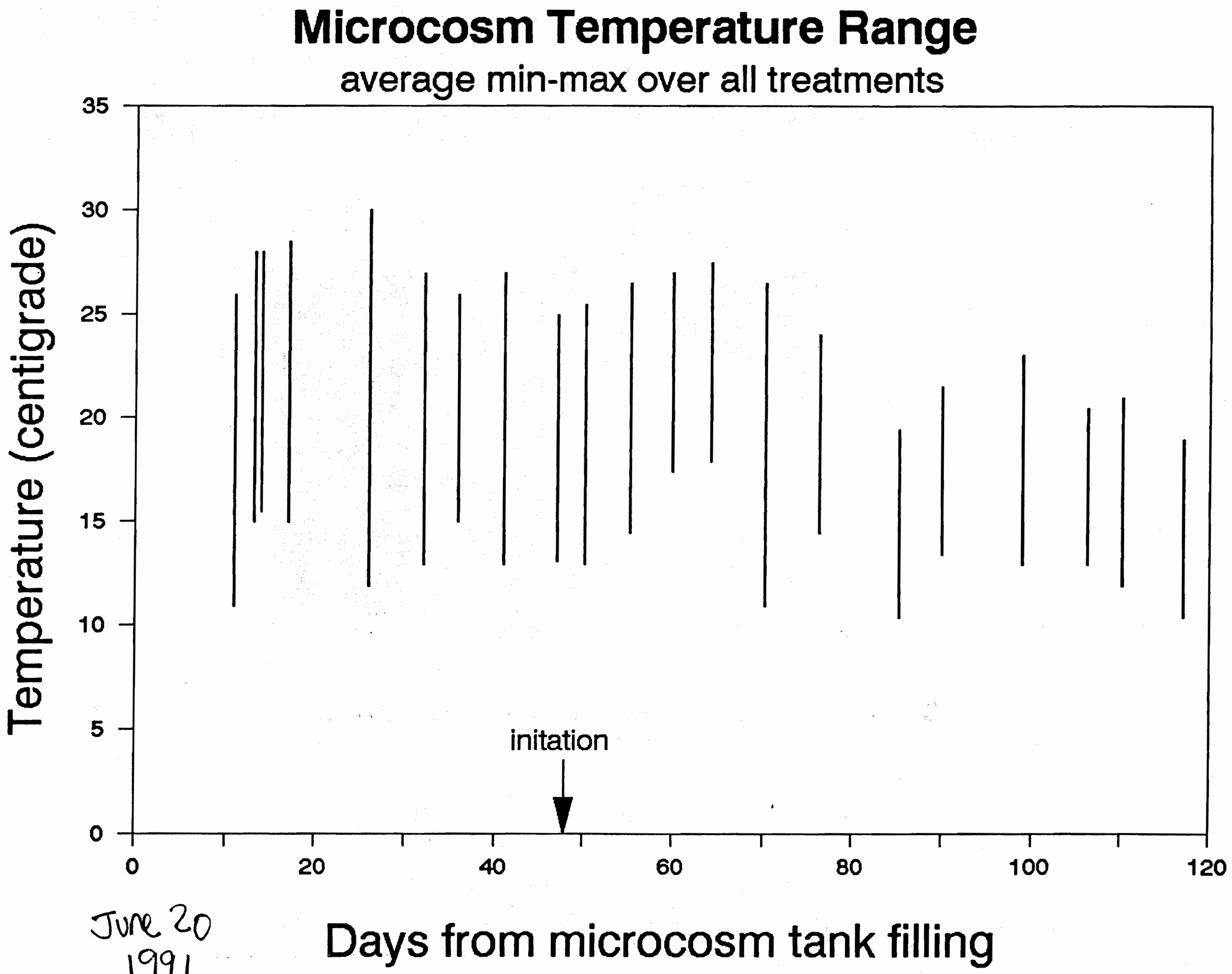
temperature range and salinity

microcosm experiments



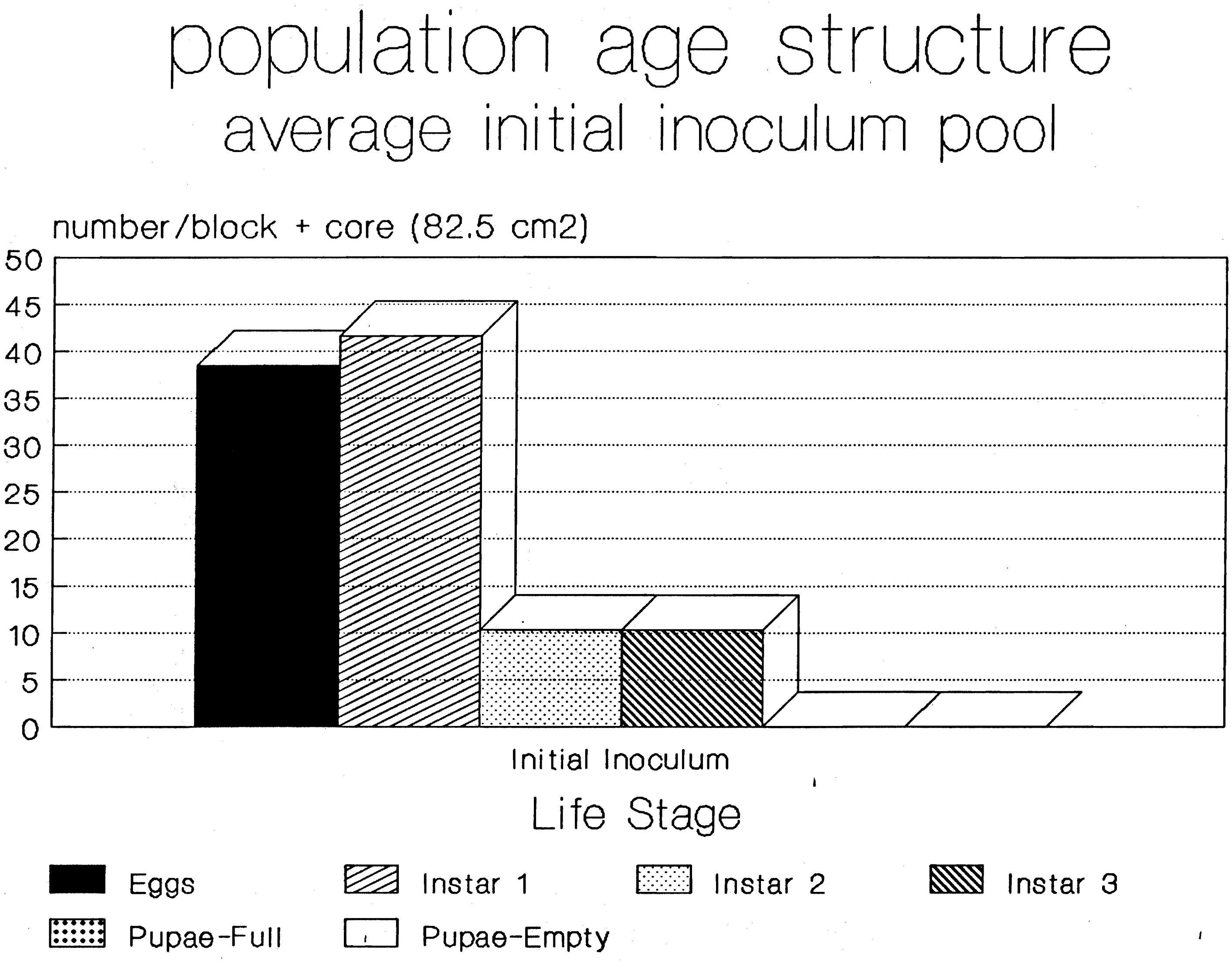
mean min-max temperature range
during experimental period:
no significant differences (ANOVA)

Figure 19



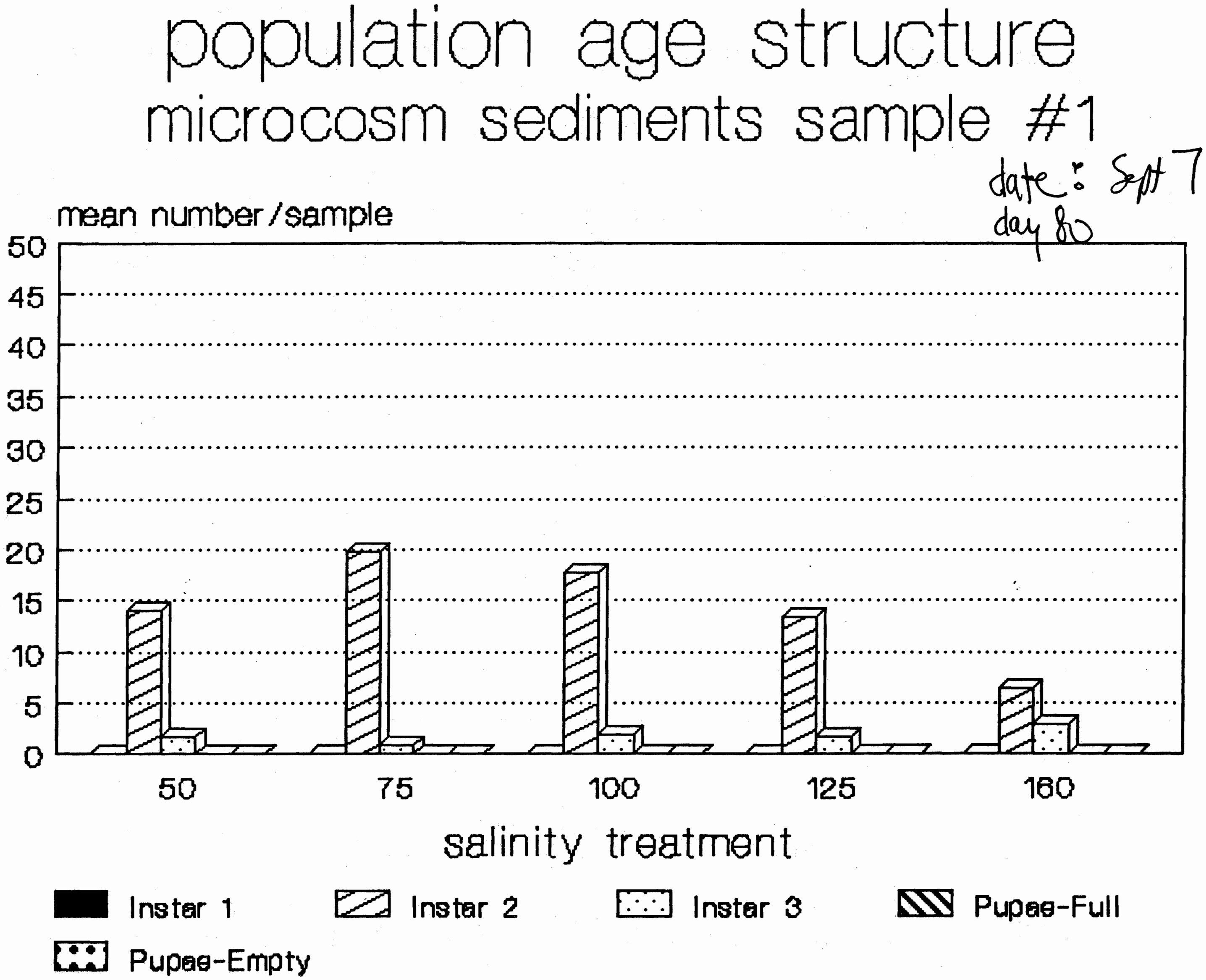
June 20
1991

Figure 2D



expected on area of 1 block + 1 core
(sum = 100 individuals/combined sample)

Figure 21



date: Sept 7
day 80

Figure 22

population age structure

microcosm sediments sample #2

date oct 9
day 112 from June 20.

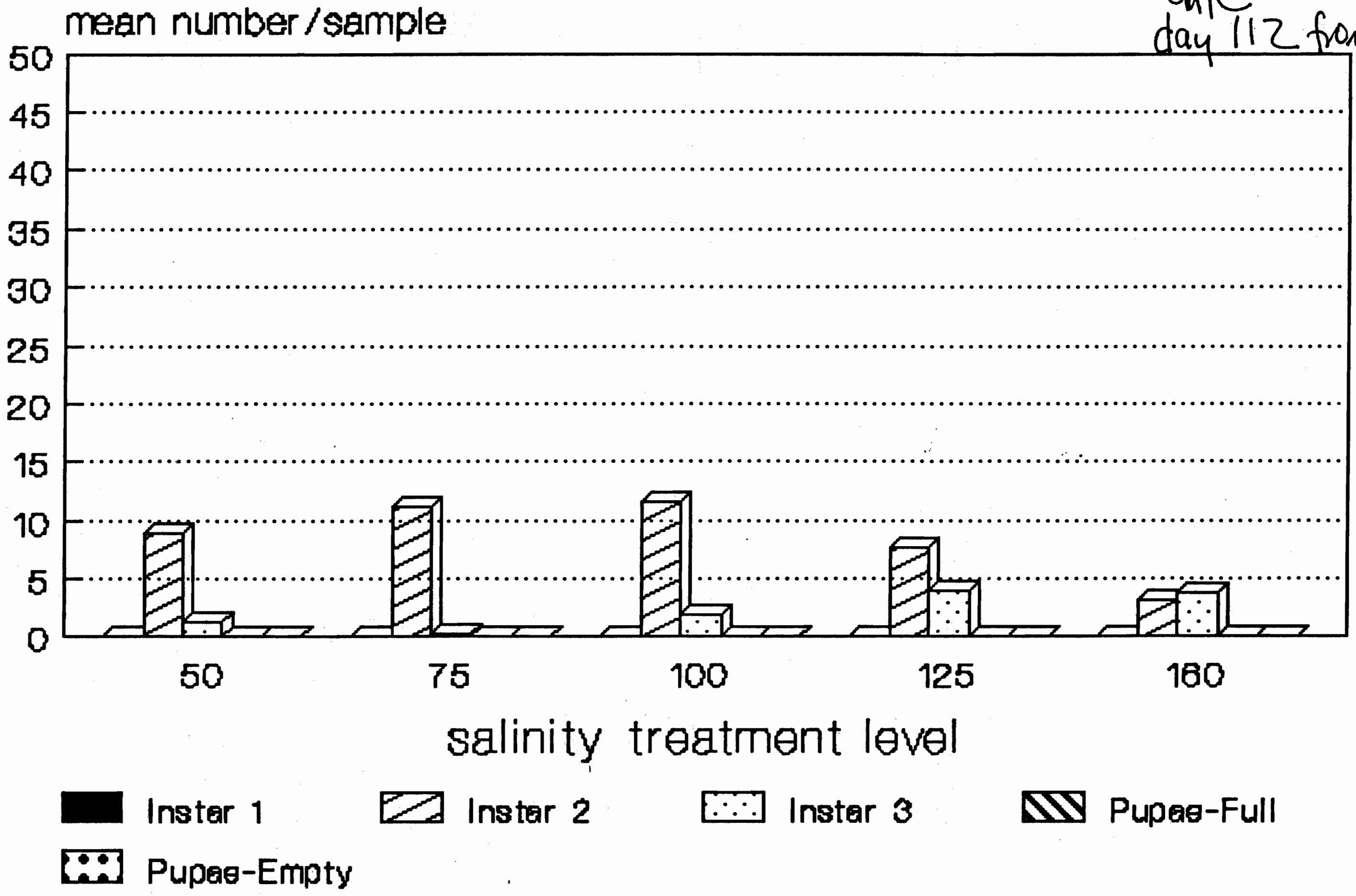


Figure 23

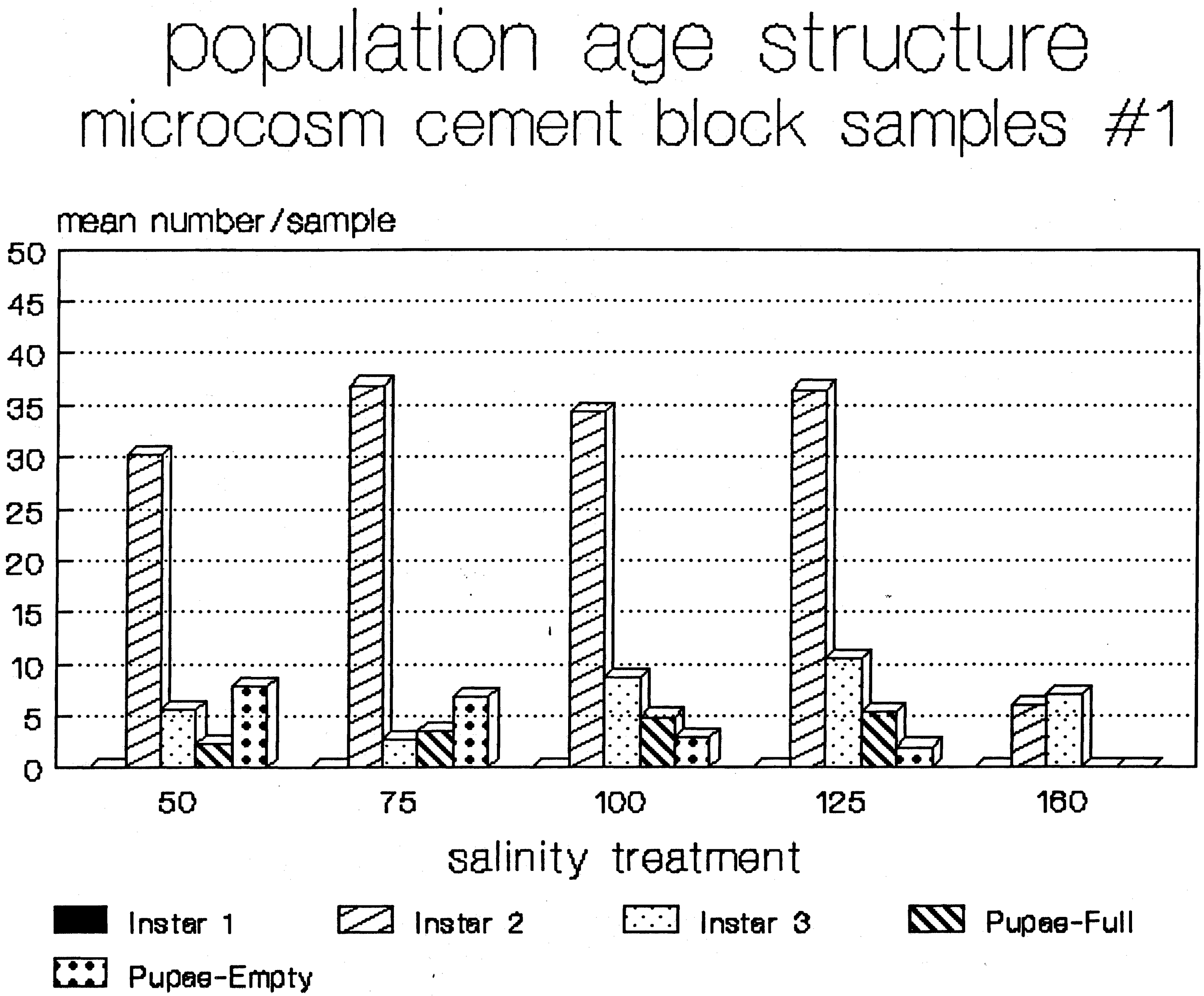

population age structure
microcosm cement block samples #1
mean number/sample
50
45
40
35
30
25
20
15
10
5
0
50
75
100
125
160
salinity treatment
Instar 1
Instar 2
Instar 3
Pupae-Full
Pupae-Empty

Figure 24

population age structure
microcosm cement block samples #2

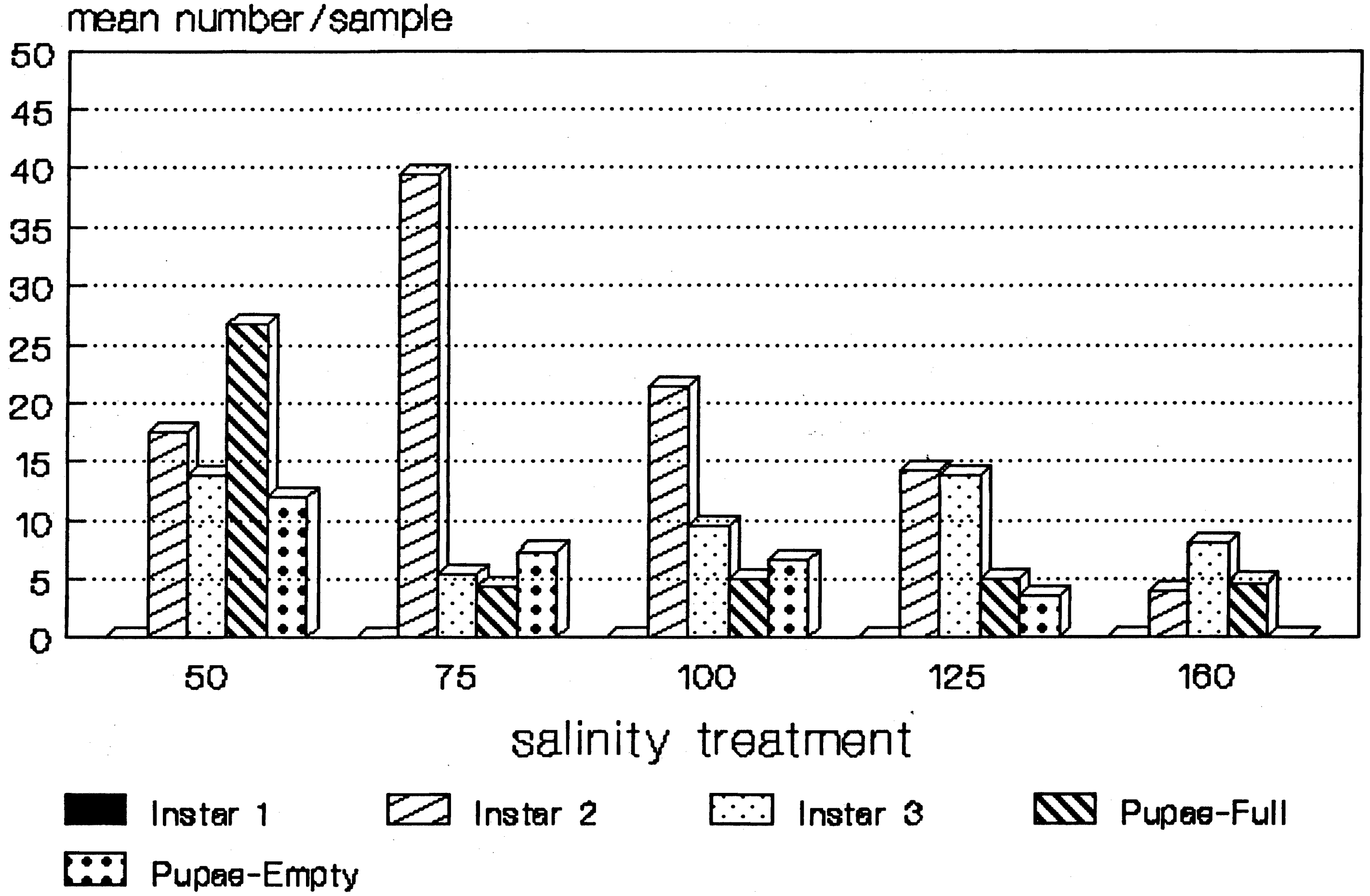
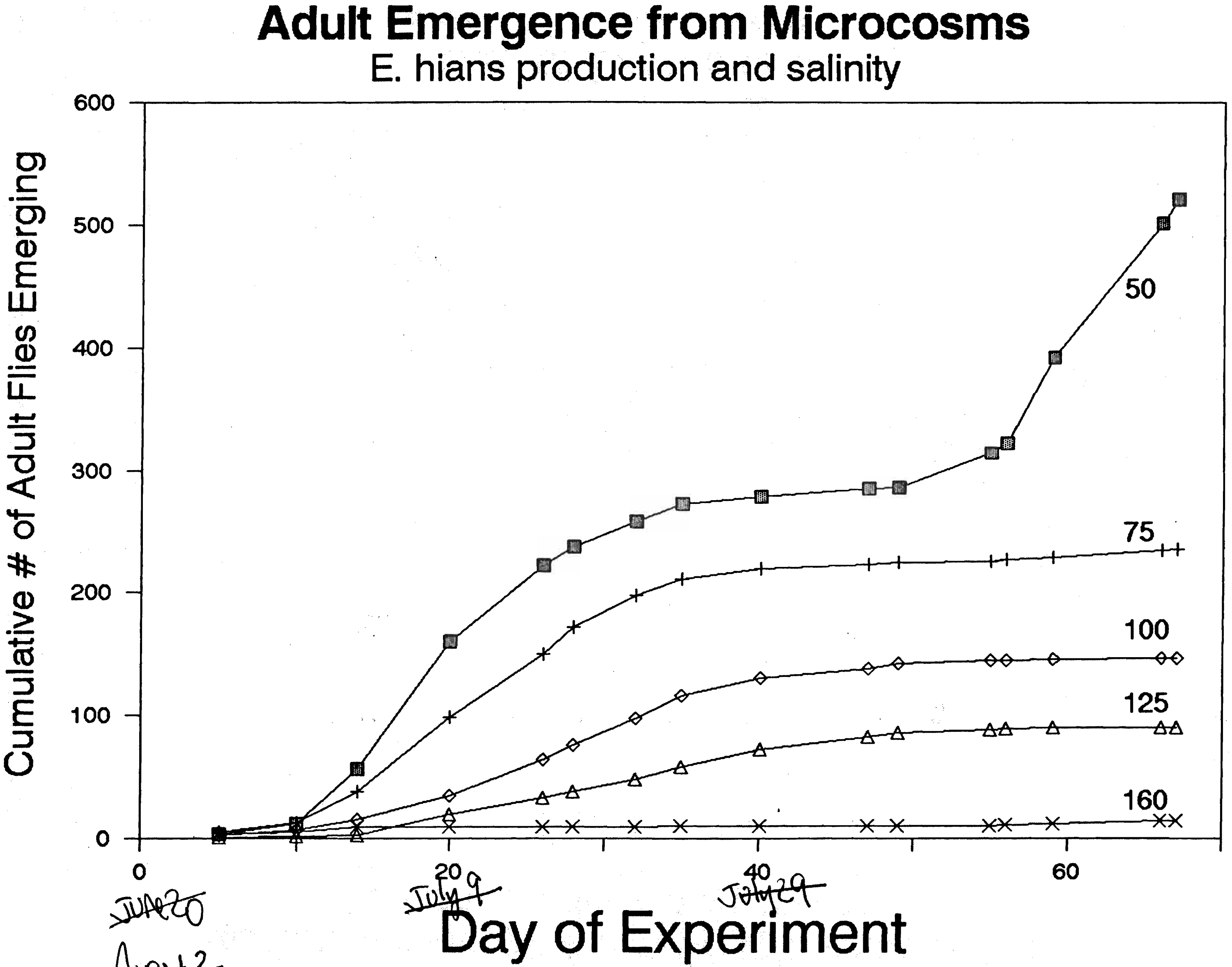


Figure 25

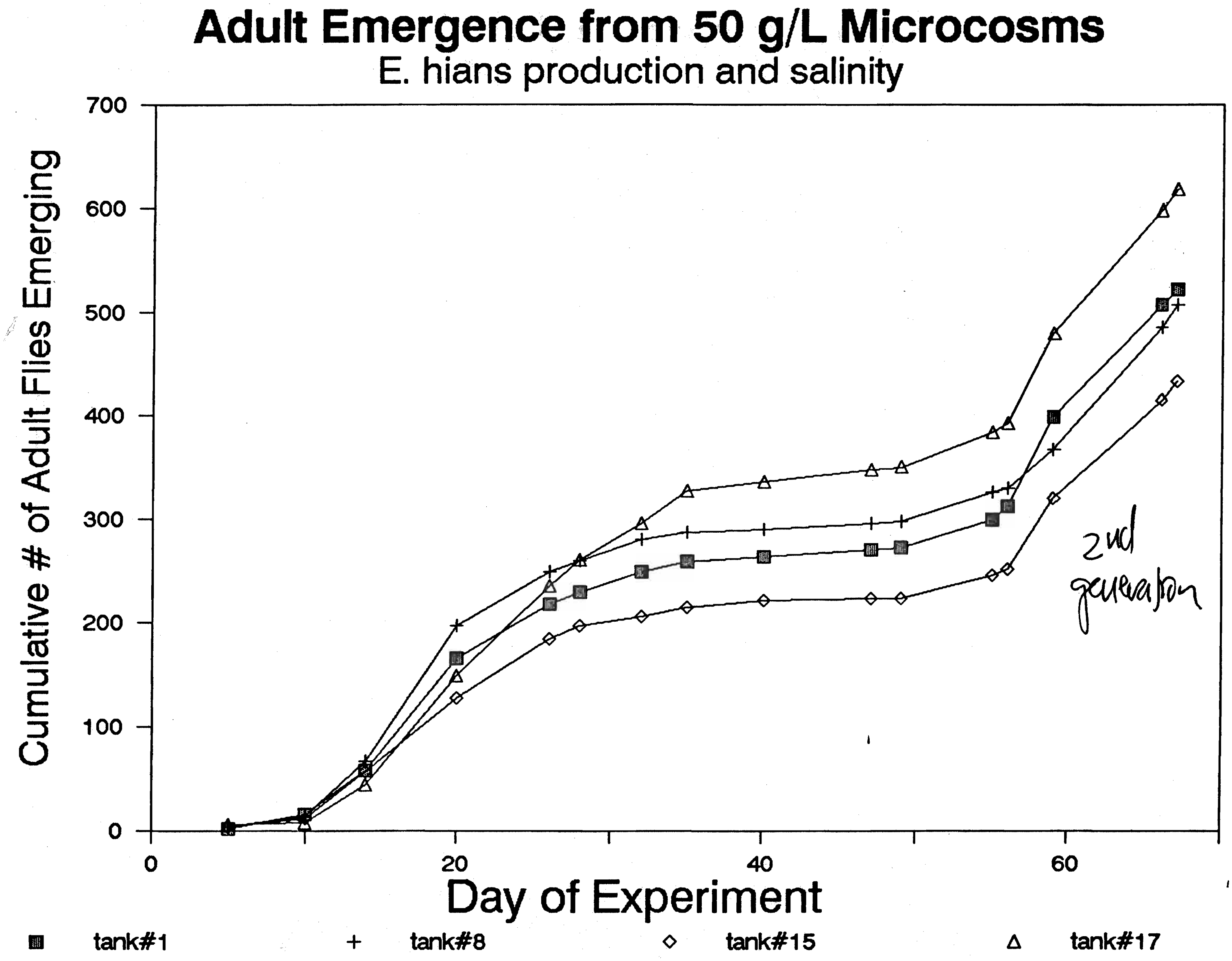


~~June 20~~ ~~July 9~~ ~~July 29~~

~~August 3~~

Initiate on day 48 after filling.
Aug 6

Figure 26



Adult Emergence from 50 g/L Microcosms
E. hians production and salinity
Cumulative # of Adult Flies Emerging
700
600
500
400
300
200
100
0
0
20
40
60
Day of Experiment
2nd generation
▨ tank#1
+ tank#8
◇ tank#15
△ tank#17

Figure 27

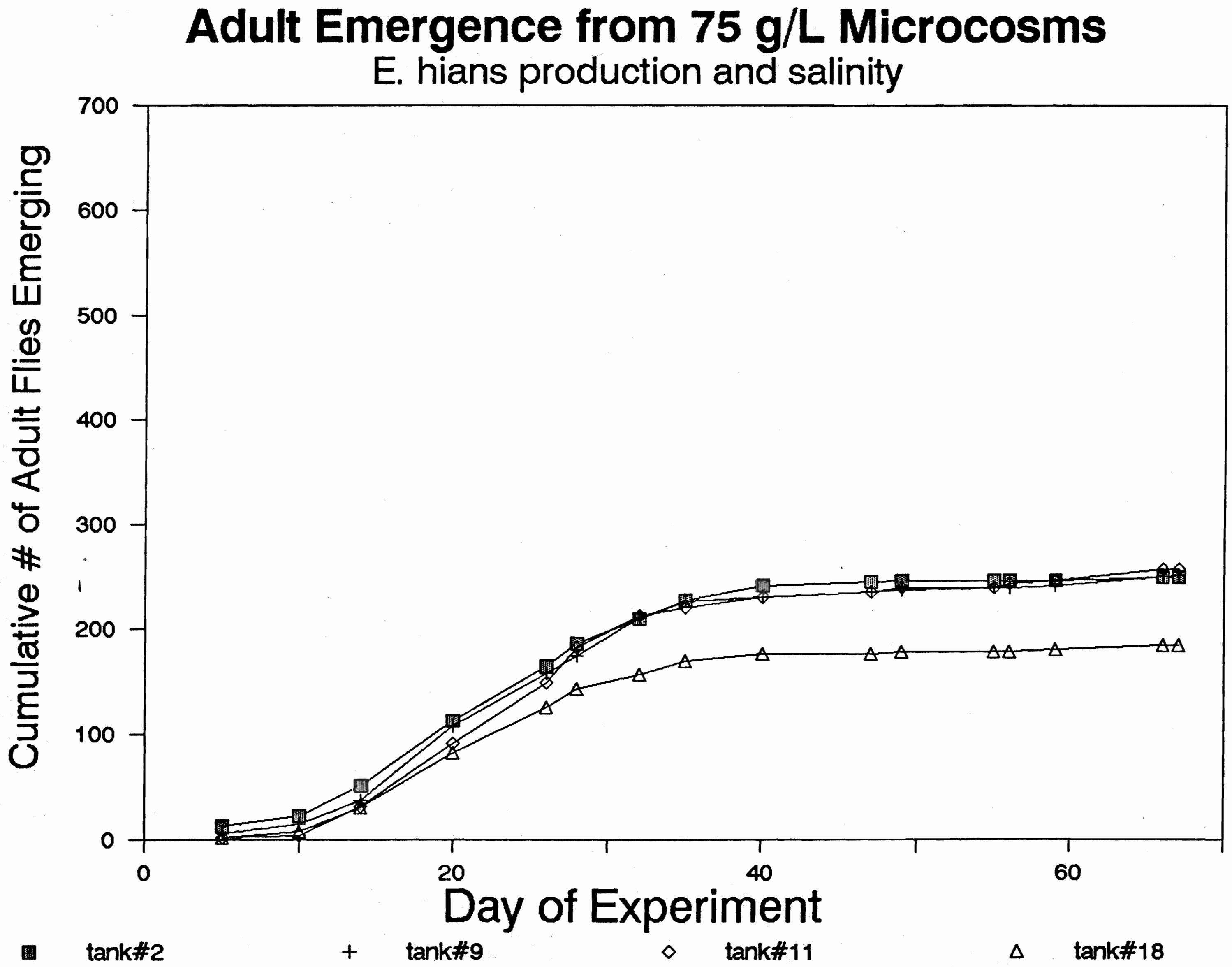

Adult Emergence from 75 g/L Microcosms
E. hians production and salinity
Cumulative # of Adult Flies Emerging
700
600
500
400
300
200
100
0
0
20
40
60
Day of Experiment
▩ tank#2
+ tank#9
◇ tank#11
△ tank#18

Figure 28

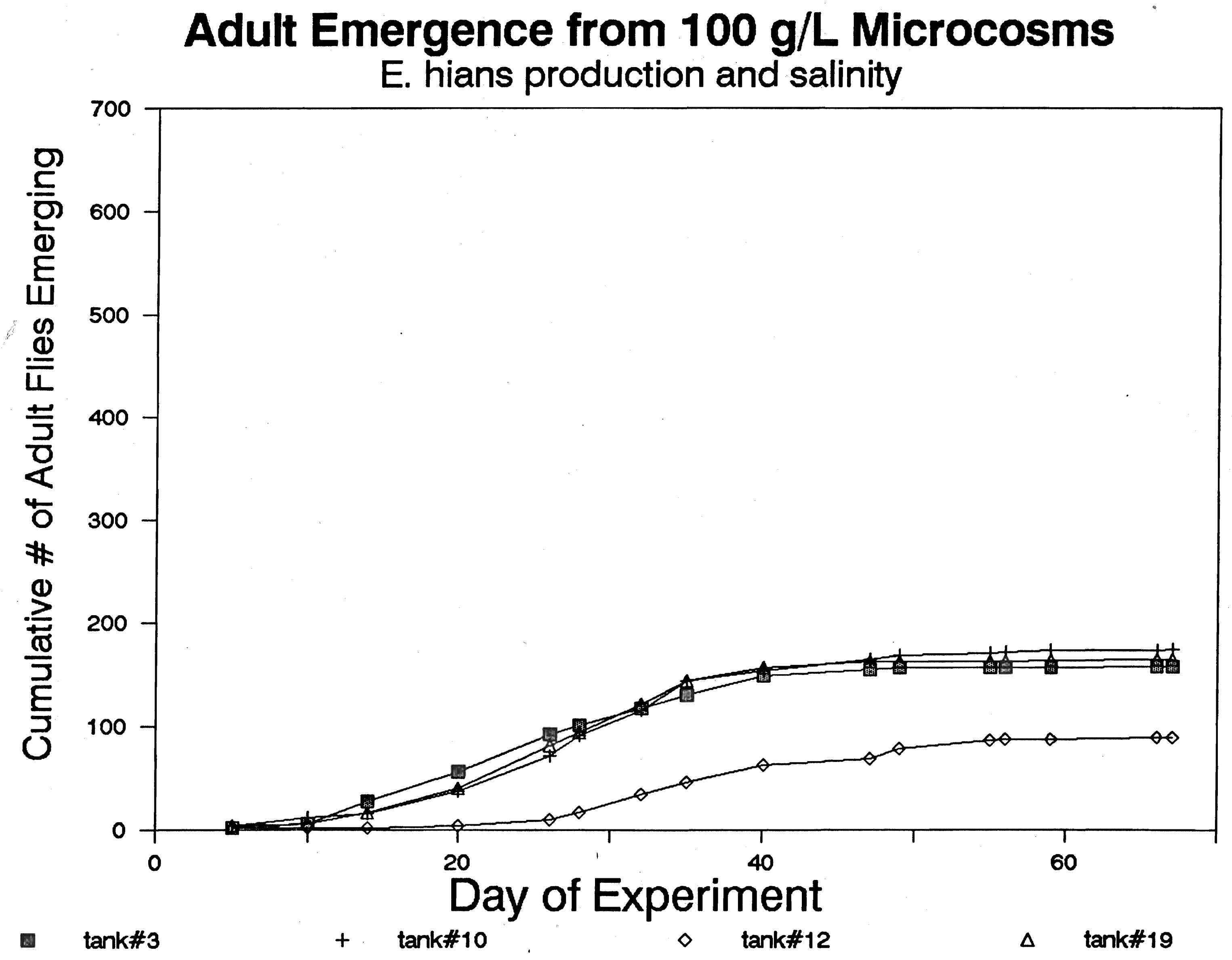

Adult Emergence from 100 g/L Microcosms
E. hians production and salinity
Cumulative # of Adult Flies Emerging
0
100
200
300
400
500
600
700
0
20
40
60
Day of Experiment
▨ tank#3
+ tank#10
◇ tank#12
△ tank#19

Figure 29

Adult Emergence from 125 g/L Microcosms

E. hians production and salinity

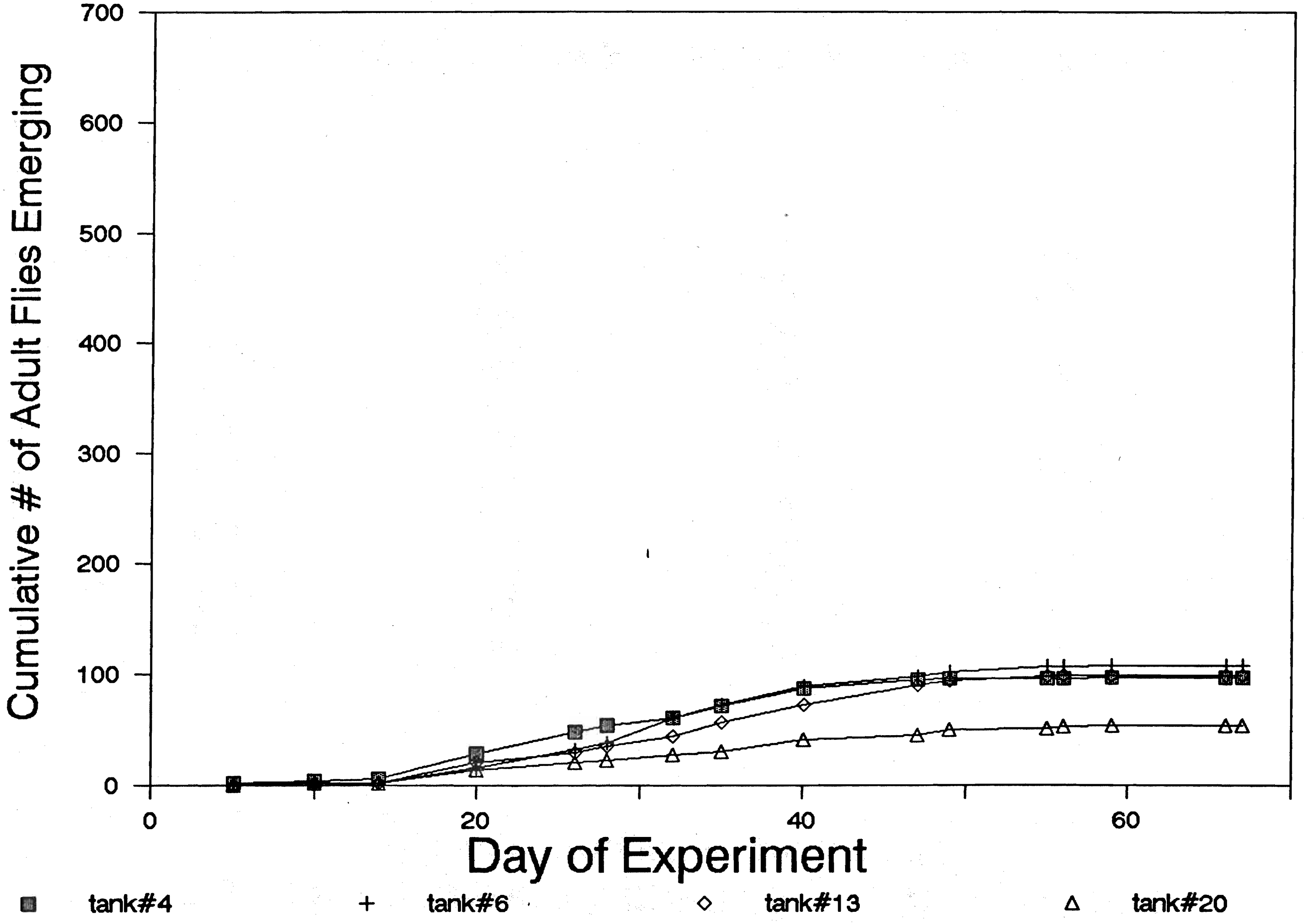


Figure 30

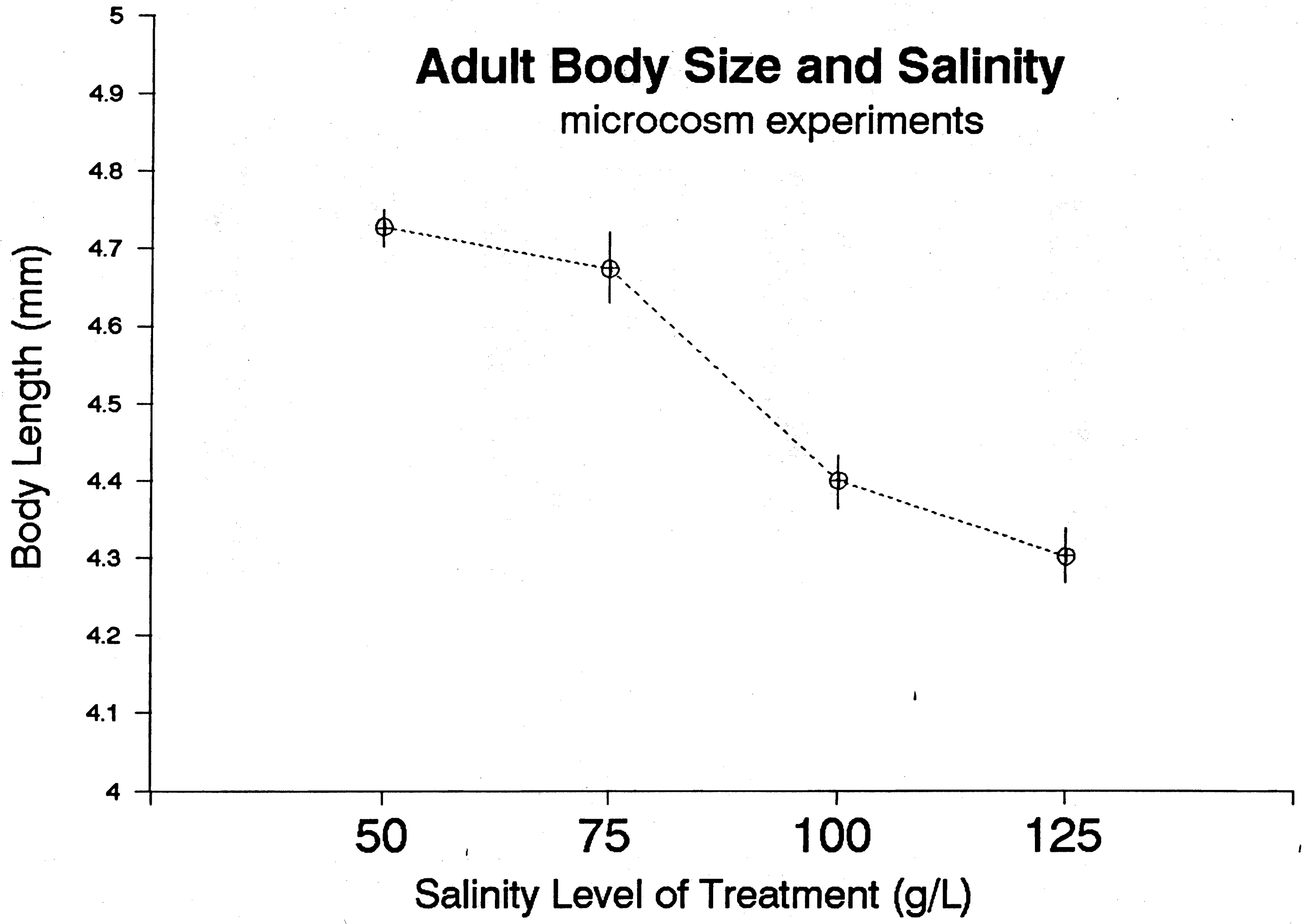
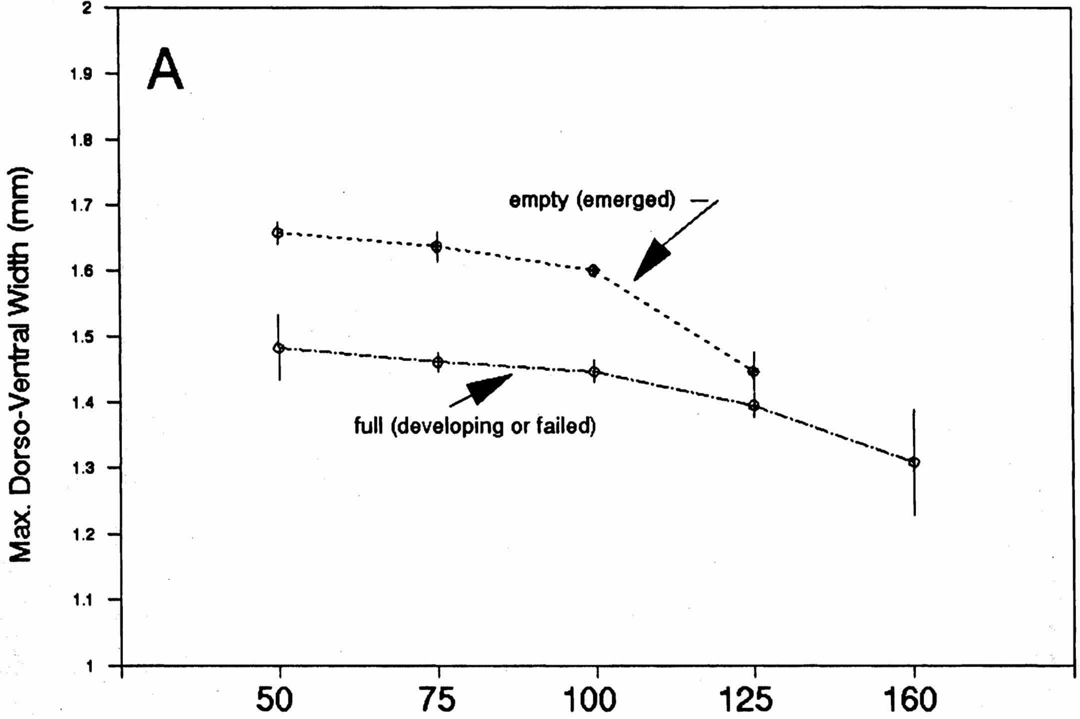

Adult Body Size and Salinity
microcosm experiments
Body Length (mm)
5
4.9
4.8
4.7
4.6
4.5
4.4
4.3
4.2
4.1
4
50
75
100
125
Salinity Level of Treatment (g/L)

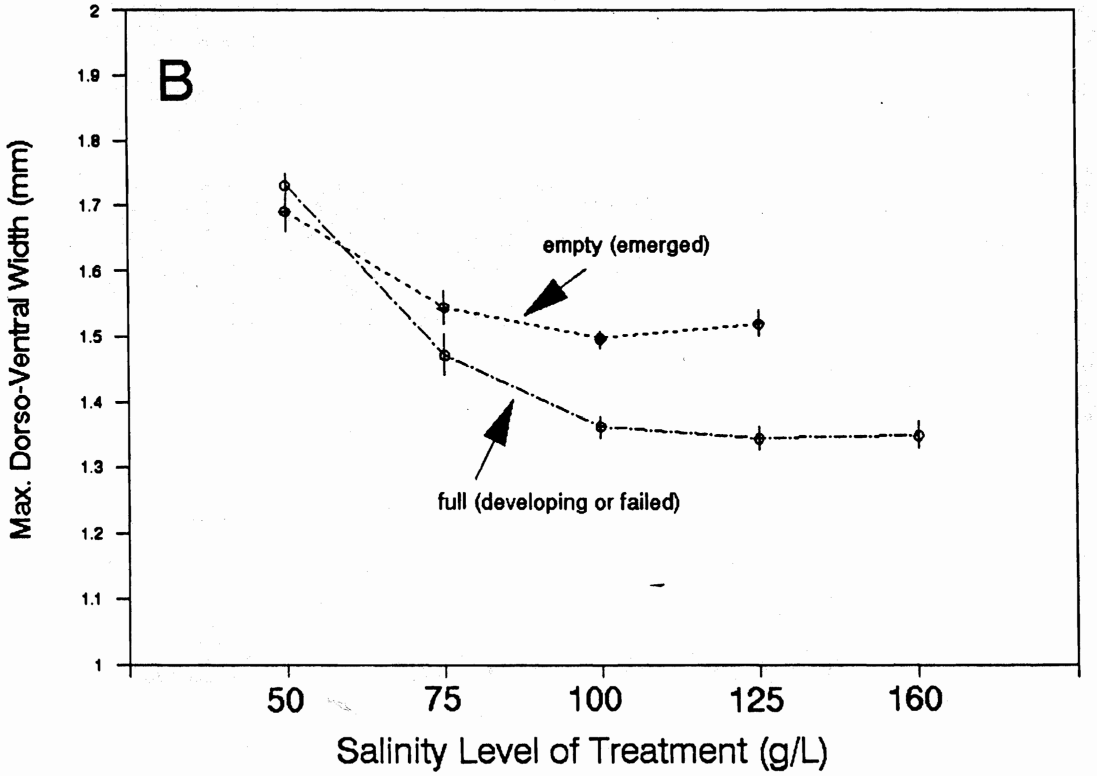
Figure 33

Figure 34



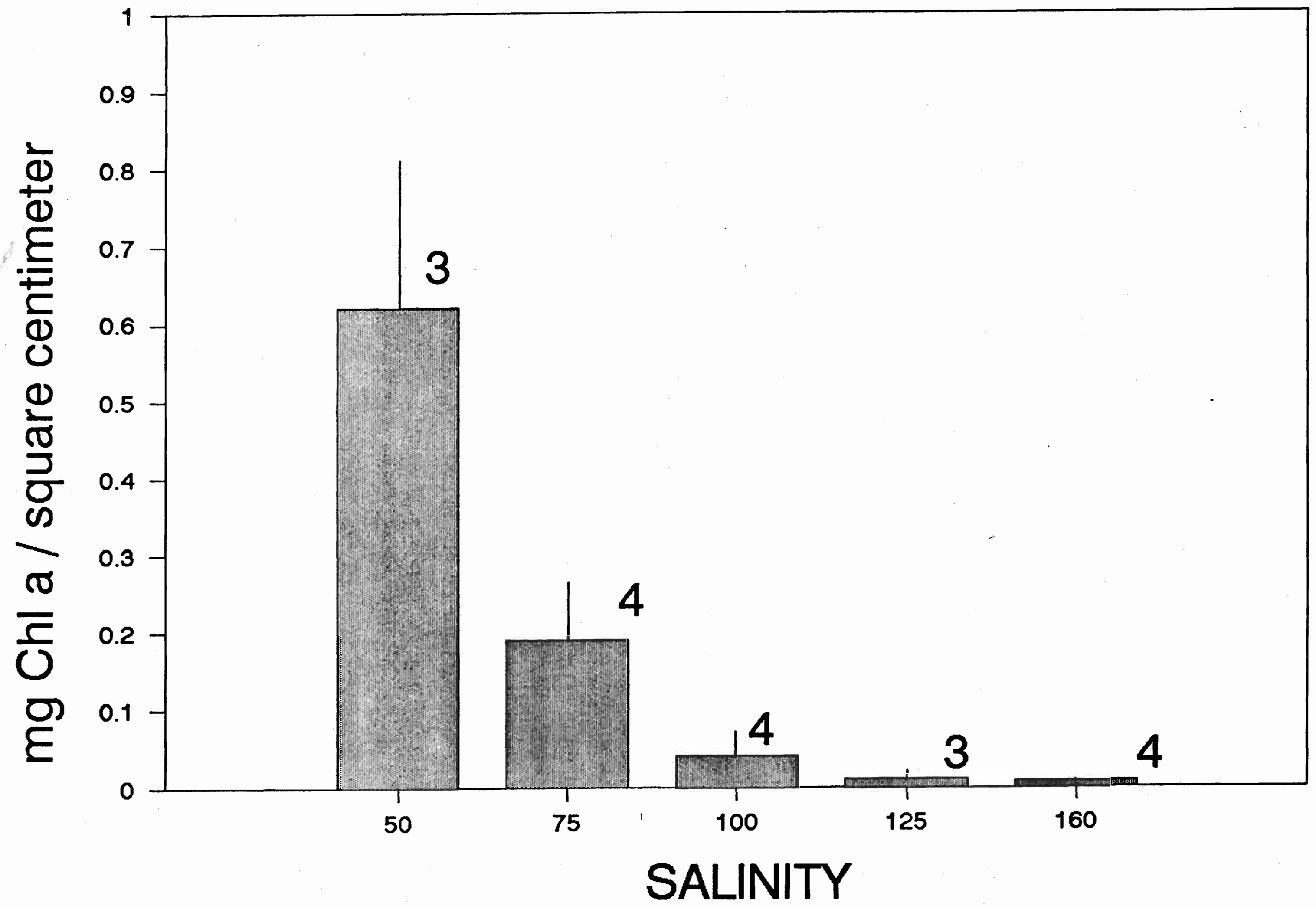
Puparium Size and Salinity: Sample 1

microcosm experiments 8 IX 91



Puparium Size and Salinity: Sample 2

microcosm experiments 8 X 91



Microcosm Chlorophyll Standing Crop

extract off microcosm airlift tubes

Figure 35

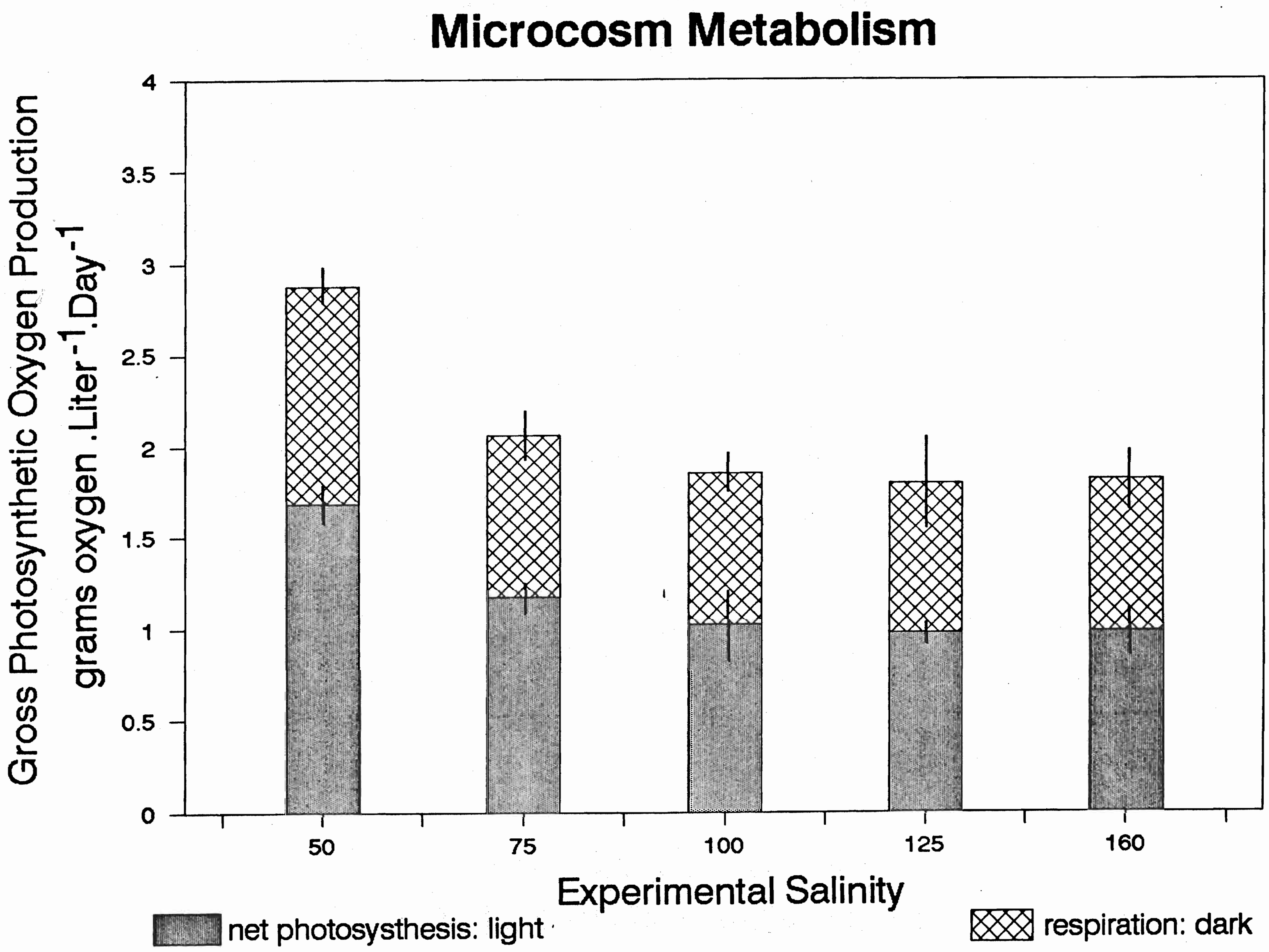

Microcosm Metabolism
Gross Photosynthetic Oxygen Production
grams oxygen .Liter^{-1}.Day^{-1}
4
3.5
3
2.5
2
1.5
1
0.5
0
50
75
100
125
160
Experimental Salinity
▨ net photosysthesis: light
▨ respiration: dark

Figure 3b

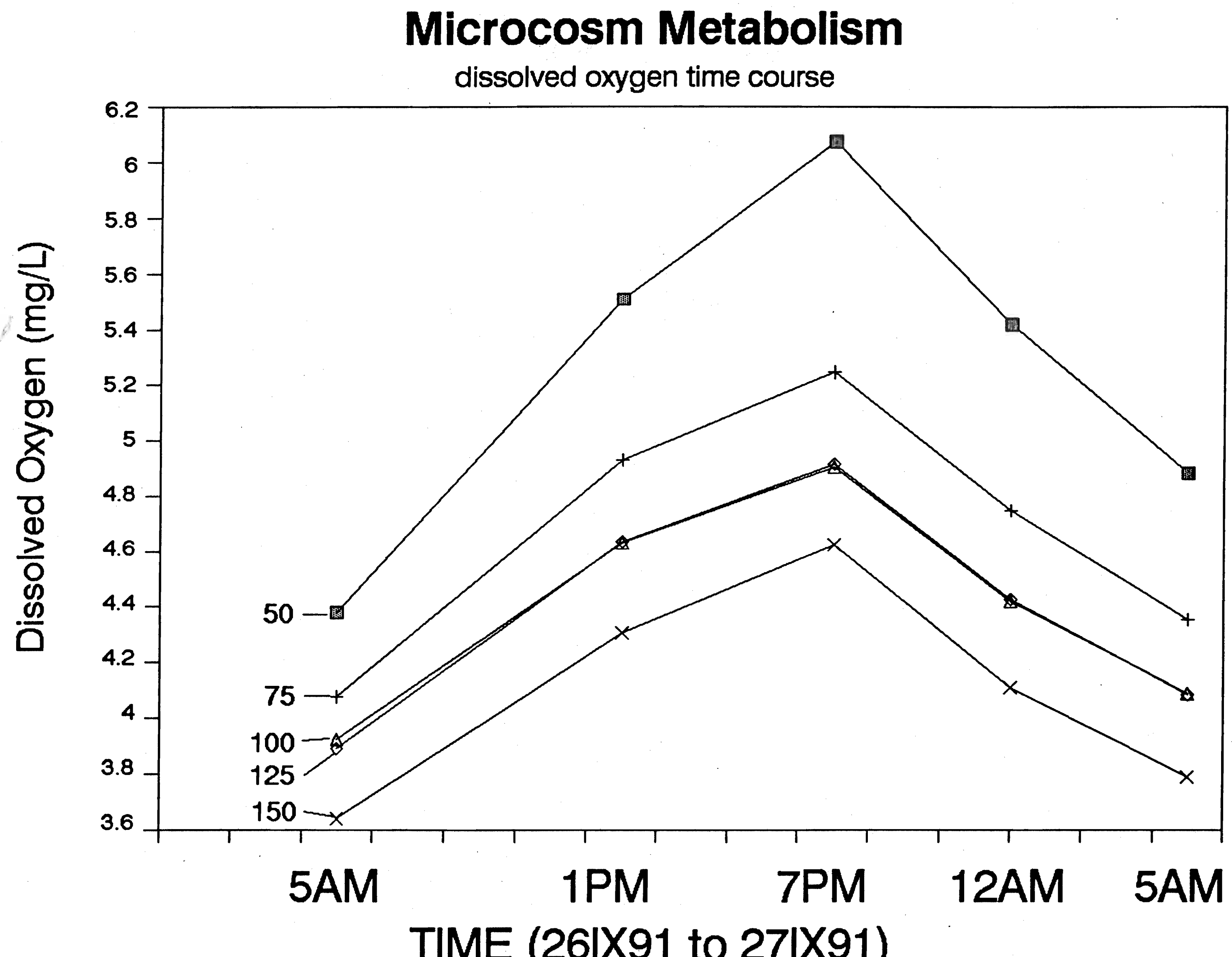

Microcosm Metabolism
dissolved oxygen time course
Dissolved Oxygen (mg/L)
6.2
6
5.8
5.6
5.4
5.2
5
4.8
4.6
4.4
4.2
4
3.8
3.6
50
75
100
125
150
5AM
1PM
7PM
12AM
5AM
TIME (26IX91 to 27IX91)

Figure 37

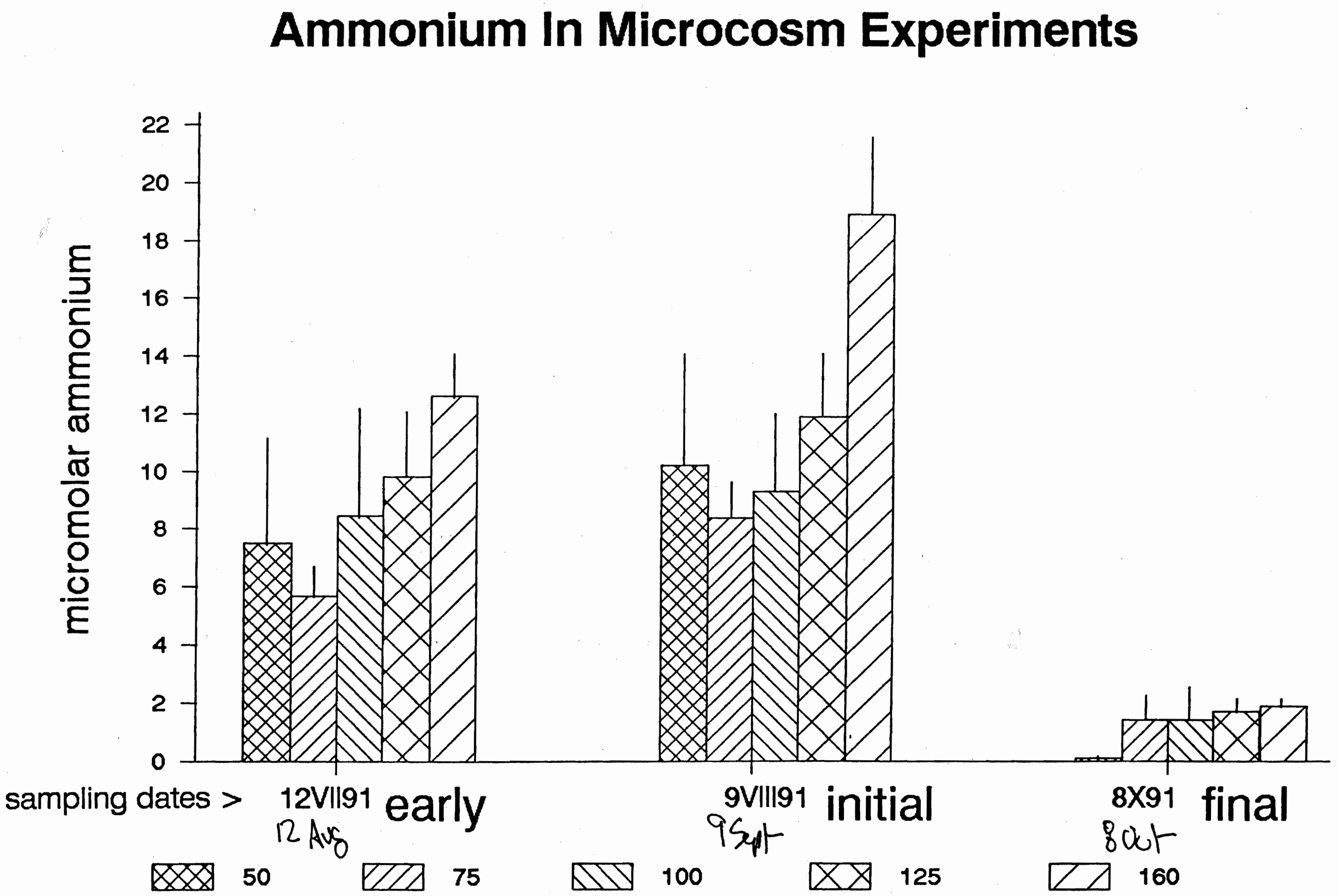

Ammonium In Microcosm Experiments
micromolar ammonium
0
2
4
6
8
10
12
14
16
18
20
22
sampling dates >
12VII91 early
12 Aug
9VIII91 initial
9 Sept
8X91 final
8 Oct
50
75
100
125
160

Figure 38