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THE ECOLOGY OF A DOMINANT EMERGENT
(TYPHA LATIFOLIA) IN A RESERVOIR

by

Robert James Hallock

A Dissertation Submitted to the Faculty of the
DEPARTMENT OF BIOLOGICAL SCIENCES
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THE UNIVERSITY OF ARIZONA

GRADUATE COLLEGE

I hereby recommend that this dissertation prepared under my direction by Robert James Hallock entitled The Ecology of a Dominant Emergent (*Typha latifolia*) in a Reservoir be accepted as fulfilling the dissertation requirement of the degree of Doctor of Philosophy

Jerry C. Tash
Dissertation Director

October 19, 1973
Date

After inspection of the final copy of the dissertation, the following members of the Final Examination Committee concur in its approval and recommend its acceptance:*

<u>William G. Nutting</u>	<u>Oct. 15, 1973</u>
<u>Floyd G. Werner</u>	<u>Oct. 15, 1973</u>
<u>Olson</u>	<u>Oct. 18, 1973</u>
<u>Charles D. Zebur</u>	<u>Oct. 26, 1973</u>
_____	_____

*This approval and acceptance is contingent on the candidate's adequate performance and defense of this dissertation at the final oral examination. The inclusion of this sheet bound into the library copy of the dissertation is evidence of satisfactory performance at the final examination.

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SIGNED: Robert J. Tallock

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ABSTRACT

Imperial Reservoir, along the lower Colorado River, is one of the major recreational areas in southwestern Arizona and southeastern California. The upper end of the reservoir is in Imperial National Wildlife Refuge, and the entire reservoir provides habitat for waterfowl and the Yuma clapper rail, Rallus longirostra, an endangered species. Approximately one-third of the reservoir and 60% of the vegetated shorelines are covered with Typha latifolia. Because evapo-transpiration may cause serious water losses in desert reservoirs, phreatophytes (including Typha) along the main channel and around the semi-isolated lakes are subject to eradication.

Typha marshes are common in temperate regions, but their fisheries have been studied only superficially. This study was initiated to define the role of Typha beds in the ecology of a reservoir and provides some information necessary for decisions regarding the future morphology of the lower Colorado River.

Comparative studies of net production among the major producers indicate that Typha blades fix more than half of the fixed energy stored by plants in the backwater communities of the reservoir. The submergent plant Najas marina was important seasonally. Benthic and planktonic algae were minor contributors, and allochthonous energy sources were also unimportant.

The distribution of Typha detritus was evaluated by long-term litter buckets, dredge sampling, and detritus studies. It was concluded

that most of the particulate Typha detritus was retained in or within a few meters of the Typha beds. Since the water level in Imperial Reservoir is essentially stable (18-in. variation) and the currents slight, the detritus formed is not flushed from the beds and transported to distant areas as it is in estuaries with strong cyclic water movements. Consequently the importance of Typha detritus as a base for food chains throughout the reservoir is much less than would be expected.

Distribution studies of invertebrates and fish indicate that the Typha beds and the Typha open-water ecotone are extremely important to the reservoir community and in particular the sport fishery.

Water movements, water analysis for carbohydrate and phenolic compounds, and laboratory extraction studies indicate that dissolved and possibly bacteria-formed colloidal contributions of the Typha beds are important to the fishery. The efficiency of energy transfer in these forms is undoubtedly low because Typha blades are nearly 50% crude fiber, which represents production not readily available. Much of the energy fixed in fiber is lost to bacterial activity before it reaches the major food chains leading to the fishery.

The extent of the use of Typha as protective cover by fish was established through sonic tagging, rotenone sampling, and electrofishing. Typha beds were found to be essential to the maintenance of large-mouth bass populations, since the bass spawn 2 months before any other cover is available for the newly hatched juveniles. The beds may also serve as actual spawning sites, influence water temperature, and help stabilize banks.

INTRODUCTION

Imperial Reservoir, along the lower Colorado River, is one of the major recreational areas in southwestern Arizona and southeastern California. The area has valuable wildlife habitat and a highly successful sport fisher, averaging more than 0.5 fish per man-hour. The upper half of the reservoir is in the Imperial National Wildlife Refuge. The refuge received 208,414 activity visits in 1971, of which approximately 25% were by fishermen (Striegler, 1972). The lower half of the reservoir probably received two or three times the recreational pressure of the upper half because of better access.

The Bureau of Reclamation has plans for channelization and phreatophyte removal along the lower Colorado River. The Bureau has proposed a series of controlled-flow lakes which would be constructed by dredging old channels and dumping the spoils on the existing marsh and backwaters. Such modification could destroy many of the large tracts of cattails (Typha latifolia) now living in the area. Typha is the most conspicuous plant in the reservoir, and it is estimated to cover 60% of the vegetated shorelines.

Typha latifolia is a perennial emergent plant ubiquitous in semi-permanent fresh and brackish water habitats of the world (Polunin, 1960). It is generally found in dense monospecific stands in shallow (less than 0.7 meters) waters. It is capable of rapid colonization of new habitats because of its ability to reproduce rhizomatically, and once established

it is extremely persistent. Being emergent, Typha has the advantages of both submerged and terrestrial plants (adequate light, CO₂, and water), and the growth is correspondingly luxurious. Marshes are considered the most productive community type in the temperate regions of the world by Westlake (1963) and Odum (1959), and the high productivity of Typha marshes has been noted in many studies (Pearsall and Gorham, 1956; Bray, Lawrence, and Pearson, 1959; Bray, 1962; McNaughton, 1966; Boyd, 1971). A thorough literature search reveals that Typha marshes are relatively unstudied with regard to fisheries.

This study was designed to evaluate Typha as a source of energy and habitat for fish and to provide data necessary for making desirable modifications of Typha marshes in Imperial Reservoir and other areas. The following objectives were considered most important:

1. To evaluate the relative position of Typha among the basic energy sources in Imperial Reservoir.
2. To evaluate the extent that energy fixed by Typha blades contributes to the fishery.
3. To evaluate the importance of physical features associated with Typha beds to the fishery.

STUDY AREA

Imperial Reservoir is a eutrophic body of water located along the lower Colorado River, long 114°27' E., lat 32°43' N., north of Yuma, Arizona. The 2,955-hectare (7,300-acre) reservoir was formed in 1938 when the Bureau of Reclamation completed Imperial Dam. The original storage capacity of 85,000 acre-feet has been reduced by siltation, and the reservoir is now used primarily for diversion (California Department of Water Resources, 1968).

Eight small "lakes" within Imperial Reservoir on the Arizona side of the river were chosen as representative study areas (Fig. 1). These lakes are actually open areas within a contiguous flooded marsh. They were formed when old meanders and the mouths of intermittent streams were flooded. Many of them are connected by open channels. These lakes are protected from natural floods and uncontrolled water-level fluctuation by the Colorado River dam system. Controlled fluctuation is about 18 in. per year. Most lakes are less than 3 meters (9.84 feet) deep, and in the summer many have extensive submerged aquatic weed beds composed primarily of Najas marina (spiny naiad). The margins of lakes 1, 3, 4, and 8 are dominated by Typha beds. Various quantities of water pass through these beds, creating a semi-open system. Study sites were chosen with respect to the estimated percentage of the shoreline covered with Typha. The surface area of the lakes studied ranged from 0.77 hectares (1.9 acres) to 7.2 hectares (17.7 acres). All lakes are holomictic because of wind action.

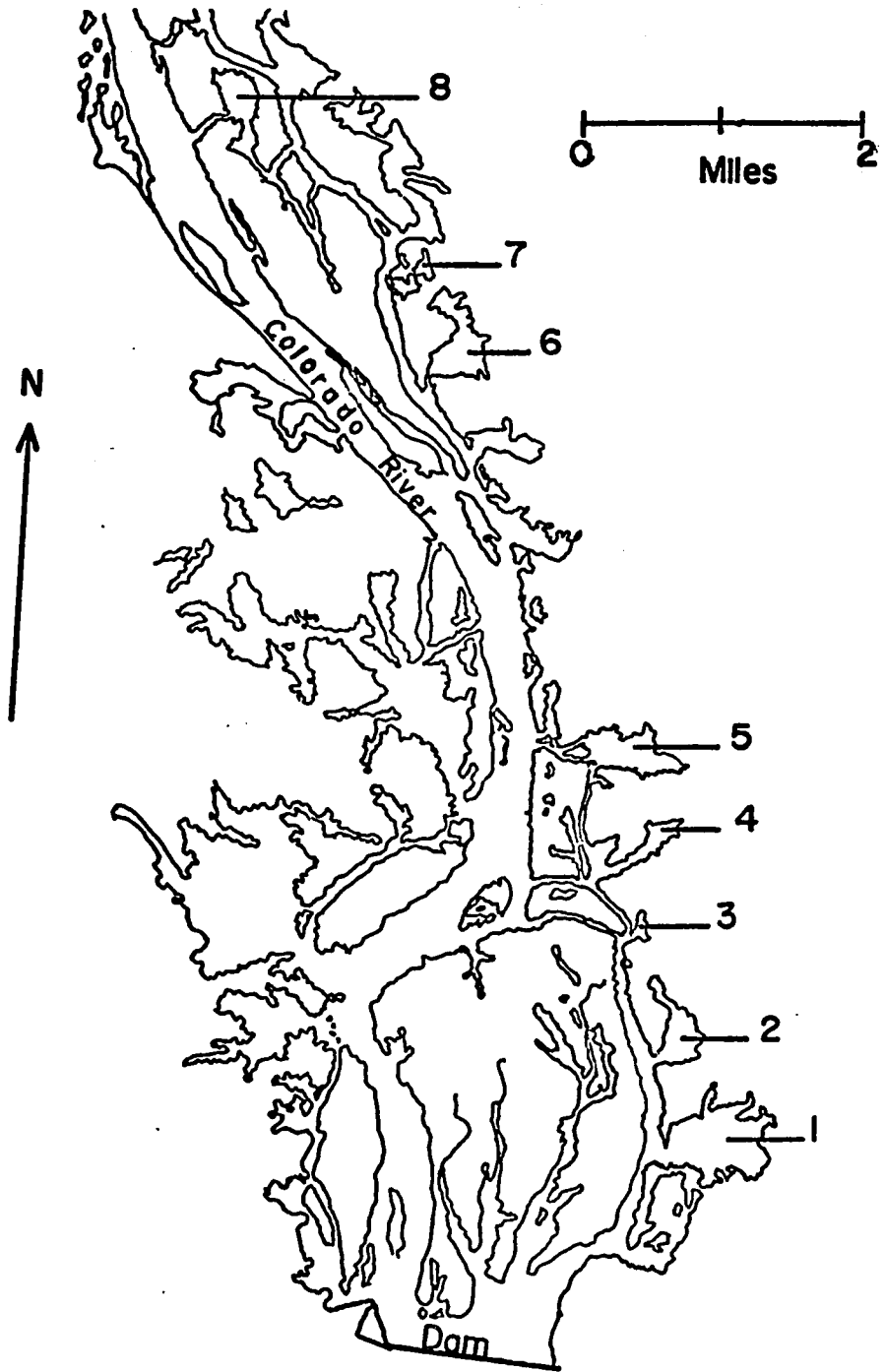


Figure 1. Study area in Imperial Reservoir

Most of the lake bottoms are composed of silt and detritus, except in those areas adjacent to cliffs and hills, where the bottom is generally rocky. Sandbars are common near lake entrances. Submerged mesquite and ironwood trees remain in most lakes. Almost every submerged object is covered with a layer of *afwuchs*.

The morphologies of lakes 7 and 8 are of particular importance to this study, since they represent the extremes found at Imperial Reservoir and since they were used for gross primary productivity studies. Lake 8 has a surface area of 2.08 hectares (5.15 acres) with an average depth of one meter. It is surrounded by extensive *Typha* beds and approximately 70% of the bottom is covered with *Najas* in the summer. The bottom is almost entirely fine silt and detritus. Lake 7 has a surface area of 0.77 hectares (1.90 acres) and an average depth of nearly 3 meters. Approximately 12% of the shore is lined with *Typha*. A thin line of *Phragmites communis* covers another 35%-45% of the shoreline, a small clump of *Scirpus acutus* occupies one end of the shore, and the remainder is primarily rocky. *Najas* covers about 70% of the bottom in the summer. The bottom is composed of fine silt and detritus grading into the rocky shores.

The desert area surrounding Imperial Reservoir has rainfall averaging about 8 cm (3 in.) per year and an evaporation rate of 195 cm (77 in.) per year (Green and Sellers, 1964). The average daily illuminance of approximately 500 g cal/cm² (U.S. Department of Commerce, 1970). Lakes isolated from the river are highly brackish with conductivities approaching that of seawater. Conductivities in the study lakes

averaged about 1500 micromohs/cm, a 50% increase above that of the main river.

METHODS

Imperial Reservoir was visited 39 times from September 1969 to September 1972. Intervals between visits ranged from 1 to 6 weeks, depending on the type of data to be collected. Measurements were made on: (1) the major energy sources in the reservoir, (2) the utilization of Typha by fishes, (3) the use of Typha beds as habitat by fishes, and (4) a few basic limnological features. The methods used are presented in the following individual categories.

Major Energy Sources

Typha latifolia

To estimate the annual production of Typha blades (leaves) a study was designed to estimate the rate of blade turnover within the population and to estimate the fall standing crop. A production estimate was not made of the underground portions (roots and rhizomes).

Typha blades frequently remain standing more than 1 year and some stand longer than 2 years. To determine the rate of turnover of blades in the population, it is necessary to separate the blades of the current growing season from those that remain standing from previous seasons. The rate of turnover among blades in the population was determined during two successive growing seasons by tagging all new blades within two 0.5 m² plots that were selected to represent average densities. Blades were tagged by attaching a small piece of 32-gauge galvanized wire through the center of the blade near the ground. At

approximately 3-week intervals during the growing season (March to October) newly sprouted blades were tagged. At the end of the growing season (October), all blades present in the plots (new and old, tagged and untagged) were counted. The total number of blades tagged during the season was determined. The ratio between the fall standing crop (the total number of blades, new and old) and the total number of new shoots tagged during the season was used as a measure of turnover rate.

To determine standing crop, Typha blades were taken from sixty-four 0.5-m² plots. There were eight plots in each of eight different sites. These sites were arbitrarily selected each year to represent the entire Typha population of Imperial Reservoir. Sampling was conducted during October of 1969 and 1970. The samples were taken by cutting, near ground level, all blades and stems within the plot. Each sample was stored in a cotton sack until analyzed. Analysis consisted of air drying the plant material for several months, oven drying it at 60°C for 24 hours, then weighing each sample to within 2%. It is desirable in biomass estimates such as these to report data as ash-free dry weight. Therefore, two 1-gram samples from a composite of the original samples were ignited in a muffle furnace at 550°C and the ash was used to extrapolate a standing-crop estimate as ash-free dry weight. To obtain a production estimate, the mean standing-crop estimate was multiplied by the rate of blade turnover.

Najas marina

The only major vascular plant other than Typha was Najas. The standing crop in October should approximate annual production because no above-soil portions overwinter and grazing by fish and invertebrates

is minimal. The standing-crop estimate was made by sampling eight areas that were selected as representative of Imperial Reservoir. Samples were taken in water that ranged from 0.5 to 1.5 meters deep. Samples were taken by forcing a galvanized metal cylinder 30.5 cm in diameter and 183 cm long through the Najas down into the bottom. All material above the bottom was scooped from the tube. After the tube was removed, the root material from the bottom down about 15 cm was removed by hand from the 734-cm² area. About 50% of the root material was recovered. The samples were stored in cotton sacks and analyzed in the same manner as the Typha blades.

Primary Production of Planktonic and Benthic Algae

Algal production was derived from measurements of diel oxygen pulses, using the method described by Odum and Hoskins (1958) as modified by McConnell (1962). A source of error in using the diel method is that it will not accurately measure gross productivity in communities containing submergent vascular plants that store oxygen longer than the period of measurement. Najas marina, a submergent vascular plant that is abundant during the summer and fall in Imperial Reservoir, stores gas (primarily oxygen) during the mornings when the plants rise in the water. The plants sink down into the water by early evening and have presumably used or voided the gas. Hartman and Brown (1967) made similar observations during experiments with Elodea canadensis and Ceratophyllum demersum. It was therefore assumed that Najas did not store oxygen for periods longer than a few hours during the middle of each day and did not contribute serious error to the measurements of gross primary productivity made during this study.

Diel oxygen measurements were made in two lakes (7 and 8) of contrasting morphology at approximately 3-week intervals for 1 year.

Oxygen measurements were made with a Yellow Springs Instrument Co., Model 5915X oxygen meter. Gross primary production was calculated using the graphical method described by McConnell (1962). Diffusion was ignored except when oxygen concentration changed more than 4 mg/l and the saturation point was within this range (McConnell, 1963). This occurred twice, and the dissolved oxygen measurements taken at these times were discarded. Dissolved oxygen measurements taken during high winds were also discarded.

To estimate algal productivity by the diel method, it was necessary to subtract the productivity of vascular plants from the total gross primary production. To subtract vascular plant production from total gross primary production, it was necessary to convert gross production to ash-free dry weight, then to net production. To convert gross primary production (expressed as oxygen evolved) to ash-free dry weight, it was assumed that each mole of oxygen evolved represents 1 mole of carbon fixed, i.e., that the photosynthetic quotient was equal to unity. Therefore, multiplying the g/m²/day of oxygen evolved by 0.375 gave the grams of carbon fixed per day. The carbon content of phytoplankton populations is approximately 50% of the ash-free dry weight (Vollenweider, 1969). Therefore, g C/m²/day was multiplied by 2.0, giving ash-free dry weight per day. The ash-free dry weight was multiplied by 365 to get an annual gross production figure.

The gross production figure was converted to a net production figure by applying a conversion factor. Odum (1957) suggests that net

production is 42% of gross production, while Vallentyne (1966) indicates that 65% might be more appropriate. An average of these two figures (53%) was used in the current study to estimate net production.

Allochthonous Energy Sources

Because Imperial Reservoir is an open aquatic system, it was necessary to measure allochthonous energy carried into the study area. The net contribution of imported energy was measured by estimating the differences between the dissolved organic material and seston in the water upstream and downstream of the reservoir.

Samples for dissolved organic material were taken monthly during the fall and winter of 1969-1970, for a total of 16 samples. Each sample was taken by removing one liter of water at the surface at each site. Samples were kept on ice in amber glass bottles and were analyzed within 24 hours of collection. All samples were filtered through an HA (0.45 μm) Millipore filter before analysis with the semimicro chemical oxygen demand (C.O.D.) method described by Maciolek (1962).

Seston was not measured within the study area proper but was estimated for all of Imperial Reservoir. Seston in the reservoir was estimated by setting nets in the currents above and below the reservoir. Seven samples were taken from January to July 1970. Samples were taken by leaving a Schuller metering tow net (#20 mesh) in the current for approximately 1 to 15 minutes, depending on the speed of the current. Approximately 5-8 m^3 water were filtered through the net for each sample. Samples were preserved in 10% formalin and returned to the laboratory for analysis.

To determine allochthonous energy in the form of seston, the samples were air dried for about 2 weeks, then oven dried at 60°C for 24 hours. The difference between oven-dried weights of samples from above and below the reservoir was used as a measure of the net contribution of allochthonous energy.

Distribution of *Typha* Detritus

To determine the distribution of *Typha* detritus, material settling out of the water was collected in litter buckets placed on the bottom in sites representative of the open-water areas in Imperial Reservoir. The litter buckets were 10-quart polyethylene buckets with a 5-pound lead weight and two 36-in. laths (as stabilizers) attached to the bottom of each bucket. Sonic recovery devices were attached to the buckets (Ziebell, McConnell, and Baldwin, 1968). Eight buckets were set in each of two transects in each of two sites (one in lake 4 and one in lake 7) for a 6-month interval. After these buckets were removed, eight new buckets were set along one of the transects in each of the two sites previously used and left for another 6 months. Of the 40 buckets set out, 25 were recovered. Material that accumulated in the buckets was analyzed for organic matter (detritus) by determining the ash-free dry weight of subsamples.

There is a possibility that the litter buckets might bias the amount of organic material that settled in them. Therefore, 20 additional mud samples were taken from two other transects (in lake 4) with an Ekman dredge. These samples were analyzed for organic matter and the results compared to those from the litter bucket studies.

Decomposition of *Typha* Detritus

Particulate decomposition of *Typha* detritus (blades only) was measured using a method similar to those of Heald (1969) and Boyd (1970a). Litter bags, approximately 25 cm on each side, made of Fiber-glas screen with 1.5-mm mesh, were packed with *Typha* blades (about two dozen 20-cm dried blade portions in each bag). To ensure fresh blade material, the blades were taken in October from an area that had burned the previous winter. Two sets of four bags each were placed in the water at each of two sites. One site (lake 7) had almost no *Typha*, steep rocky sides, and very little submerged vegetation. The other site (lake 4) was in the center of an extensive *Typha* bed. The bags were submerged in December 1970, and one bag was removed from each site every 3 months. After removal, the bags were rinsed free of silt and all macroorganisms were removed. The rate of decomposition was determined by analysis of crude fiber and nitrogen content. The results were expressed as percent of the dry weight of the subsample. Nitrogen was measured by the Kjeldahl method (American Public Health Association, 1965) and crude fiber by the standard method given in Methods of Analysis (Association of Official Agricultural Chemists, 1965).

Dissolved organic material was measured in open water in the study area and in water entering the study area from adjoining *Typha* beds. Fourteen samples for carbohydrate and phenolic analysis were taken during the period from November 1969 to April 1970, seven each from the open-water areas and from the adjoining *Typha* beds of the study area. These samples were collected in the same way as previously described for total dissolved organic material. The phenol-sulfuric acid

method was used to determine total dissolved carbohydrates (Dubois et al., 1956). The tyrosine technique (American Public Health Association, 1960) was used for total phenolic measurements.

To determine the maximum rate of leaching of organic material from Typha after it falls into the water, an extraction experiment was initiated. Dried Typha blades from the current year's crop were oven dried at 60°C for 2 hours, weighed, and mixed with tap water in a blender, then diluted to 0.029 mg/l with tap water. There were two phases of the experiment, one for phenolic compounds (1-day duration) and another for carbohydrates (6-day duration). Three replicates were run for each phase. The temperature of the dilution was kept at 6°C to retard bacterial growth.

Utilization of Typha Detritus by Invertebrates and Fishes

Benthic insects were sampled with an Ekman dredge in spring, summer, and fall. Samples were taken in the center and at the edge of Typha beds of lake 4. All samples were rinsed in a 30-mesh wash bucket and preserved in 10% formalin. Ten large midge larvae (Chironomus sp. and Clinotanypus sp.) were removed from each sample, crushed on a glass slide, and their stomach contents analyzed.

Asian clams (Corbicula fluminea) from 2 to 4 cm long were collected by hand from Typha beds along the main channel near lake 2 and from the open water of lake 1. Twelve clams from each area were preserved in 10% formalin. Their stomachs were removed and the contents examined.

Plant portions in stomach contents were identified by comparing contents to slides made from the cuticles of known vascular plants. These slides were prepared with the procedures outlined by Storr (1961), as modified by Anthony (1972).

During the summer of 1971, 51 fish were collected in the proximity of Typha beds at lakes 1, 2, and 6 for qualitative stomach analysis. Only fish larger than 11 cm were kept for this purpose. Twelve largemouth bass (Micropterus salmoides), 14 bluegill sunfish (Lepomis macrochirus), 13 red sunfish (Lepomis microlophus), 6 channel catfish (Ictalurus punctatus), and 6 carp (Cyprinus carpio) were examined. Most were taken along the shore with electrofishing gear. On one occasion, an experimental gill net was used. The stomachs were removed within 20 minutes and preserved in 10% formalin, and the contents were later identified.

Use of Typha as Protective Cover by Fishes

The role of Typha as protective cover for fish was studied through in situ visual behavior observations and with telemetric tracking. Telemetry was used to track three largemouth bass (Micropterus salmoides). The bass were collected from the reservoir with hook and line. Fish in excess of 38 cm (15 in.) were used for tag implantation. Transmitter tags (15 mm x 44 mm) were implanted, using the procedures and equipment of Ziebell (1973). Pre-implantation tests of transmitters indicated that they gave very strong signals at distances in excess of 150 meters. Fish were held for observation 10 to 12 hours after the operation and were released only after it could be ascertained that they would

survive. Two fish were released in each of two lakes (lakes 4 and 6). Fish were found and tracked for 67 hours.

Limnological Measurements

Alkalinity was determined titrimetrically with the procedures outlined by the American Public Health Association (1965). Hydrogen ion concentrations were determined with a LaMotte color comparator. Temperatures were taken with a Yellow Springs remote reading thermometer. Conductivity was measured with a portable meter, WH Curtain Model RD-152. Light penetration as percent transmittance was determined with an O.R.T. Model 504 submarine photometer.

RESULTS

Typha latifolia, Najas marina, algae, and allochthonous material are the major potential sources of energy for the fishery of Imperial Reservoir. The data collected on the relative energy contributions and on the environmental relationships of these vegetative types to the fishery are presented in the following sections.

Major Energy Sources

Typha latifolia

On a surface area basis, Typha beds are by far the most productive component in the reservoir (Table 1). Some portion of the current year's production was stored in the rhizomes and not represented in blade growth, while early blade growth resulted from energy stored in the rhizomes from previous season(s). It is assumed that these energy contributions and losses are similar for each season's crop and are self canceling because only established communities were sampled. Occasionally large chunks of root material are found floating in the lakes, but most of the root material decomposes in situ underground. The Typha blades appear far more important than roots as an energy source to the above ground marsh community.

Penfound (1956) and McNaughton (1966) report that few if any blades remain standing as long as a year within Typha marshes in areas with pronounced winters. At Imperial Reservoir, blades were observed to fall throughout the year, and some blades remained standing more than

Table 1. Productivity of major vegetative types in Imperial Reservoir

Producer	g O ₂ /m ² /day	g C/m ² /day	Ash-free Dry Weight (net)	
			g/m ² /day	kg/m ² /year
<u>Typha</u> blades			5.20	1.81
Submerged community	5.53	2.07	2.20	0.80
<u>Najas</u>			1.20	0.44
Algae ^a			1.00	0.36

a. Algal production is derived from the productivity of the submerged community by subtracting estimated Najas production. This figure is probably an overestimate.

18 months (Fig. 2). There was no evidence of grazing upon the bases of new blades and only a few instances of grazing, probably by insects, upon the upper portion of blades. Strong winds and the activities of large animals were the main causes for blade losses in the sampling plots. On two occasions blades were broken down in the tagging plots by large animals, apparently cattle, beaver, or humans (fishermen). Strong winds were reported in the Yuma valley 20 miles south of the study area between all sampling periods (U.S. Department of Commerce, 1970). Strong winds were defined as those averaging greater than 4 miles per hour for 24 hours. Such winds occurred twenty times during the 1970 blade bagging study, occurring every month. In this area, winds are generally gusty and at times greatly exceed the average. No

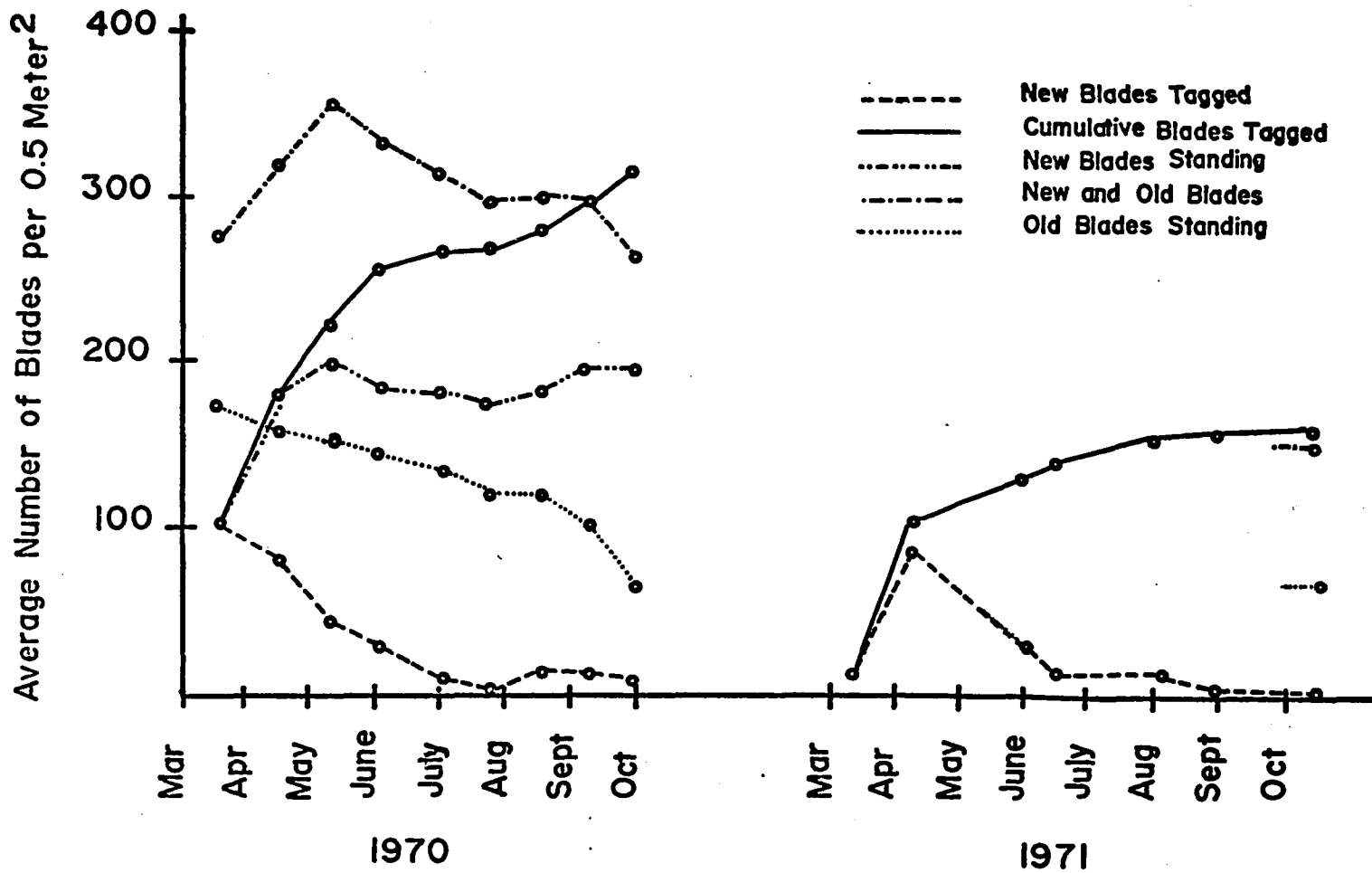


Figure 2. Typha blade turnover for 1970 and 1971 at Imperial Reservoir

evidence of mass blowdown was observed. Most of the falling blades were dead, from both the current and previous seasons. Green blades appeared to resist falling. A large proportion (25% to 40%) of the new blades died and fell before October.

The growth rate was most rapid in March, as would be expected since this was a southern population. In Oklahoma, Penfound (1956) found the growth rate to be most rapid during May. McNaughton (1966) found growth rates to be fastest in July and August in two Oregon Typha populations. Growth was initiated about the first of March in 1970 and the fifteenth of March in 1971. These dates are similar to those reported by McNaughton (1966) and Penfound (1956) for numerous populations in western United States.

New blades stopped appearing in July but were again evident in August and September (Table 2). This growth pattern can be attributed to the response of southern Typha populations to day length and temperature (McNaughton, 1966). The fall blades help support the remaining standing Typha blades during the winter.

Numerous authors (Bray, 1962; Westlake, 1963; McNaughton, 1966; Boyd, 1971) have reported Typha blade production as dry weight. Their studies were based on periodic samples taken throughout the growing season. Such productivity estimates do not include blades that are lost between sampling times and are therefore underestimates.

In this study, the standing biomass estimates were corrected for blade turnover (losses and blades remaining from the previous season as described in Methods). The annual blade turnover rate was 1.17 in 1970 and 1.07 in 1971 for an average of 1.12; that is, production was

Table 2. Concentrations of total phenolics and carbohydrates found in the water in and adjacent to Typha beds during 1969 and 1970

Date	Total Carbohydrate (mg/l)		Total Phenolics (mg/l)	
	In <u>Typha</u> Beds	Adjacent Open Water	In <u>Typha</u> Beds	Adjacent Open Water
Nov. 8	1.5	2.0	0.1	0.0
Nov. 22	0.5	2.1	0.6	0.2
Dec. 14	0.5	1.0	0.4	0.0
Jan. 11	2.1	2.3	0.0	0.0
Feb. 7	1.0	1.0	0.0	0.0
Mar. 22	1.0	1.5	0.0	0.1
Apr. 18	1.7	1.0	0.0	0.0

1.12 times the standing biomass of all blades remaining in October (Fig. 2). The greatest range in standing biomass was found in 1971, when the extremes of 1.04 and 3.5 kg/m² were recorded. Most values are close to the two-season mean of 1.82 kg/m².

Annual production estimates derived by multiplying standing biomass data by 1.12 were 1.84 (1970) and 1.77 (1971) kg/m² ash-free dry weight, for an average of 1.80 kg/m². The mean biomass of blades in late fall was 1.82 kg/m² (1970) and 1.75 kg/m² (1971) dry weight. The ash content of blade material was 9.4%. The standing biomass as ash-free dry weight was 1.65 (1970) and 1.58 (1971) kg/m². Data in

this study and that of Westlake (1966) showing that Typha blades are approximately 9% ash can be applied to the dry weight production figures reported by McNaughton (1966) to give extremes of 1.20 and 13.65 kg/m² ash-free dry weight per growing season. All other total production figures given by the above-mentioned authors are within these limits, and most are near the lower end of the range. Since most of these authors have not fully accounted for new blades that were lost during the growing season, it is likely that their data underestimate actual blade production.

Najas marina

Najas marina has a growing season of approximately 3 months (mid-June to mid-September) in Imperial Reservoir. In this study, the fall standing biomass (as equated to net production by Westlake, 1966) was 0.49 kg/m² as dry weight (0.43 kg/m² ash-free dry weight). Net production per day averaged 4.13 g/m² for about 105 days. Little grazing was observed on the spring vegetation during this season. The proportion of energy stored in root material was probably less than 10% (Westlake, 1966).

Algal Primary Production

The diel oxygen method measures gross primary production of the entire submerged plant community. During 1969-1970, gross primary production, on a surface area basis, ranged from 0.22 to 4.0 g O₂/m²/day in lake 7 and 1.20 to 8.20 g O₂/m²/day in lake 8. In both lakes, the lowest levels were in February and the highest were in late July and early August. Productivity was consistently higher in lake 8, but it followed similar seasonal patterns in both lakes.

Gross primary production for the submerged community averaged 2.10 and 4.75 g O₂/m³/day in lakes 7 and 8, respectively (Fig. 3). This difference was significant at the 5% level using Student's T test. The averages, on a surface area basis, are 6.30 (lake 7) and 4.75 (lake 8) g O₂/m²/day, and again, this difference was significant. For Imperial Reservoir as a whole, gross primary productivity averaged 5.53 ± 0.77 g O₂/m²/day. In the only comparable studies in other desert waters in this area, McConnell (1963) found an average of 4.40 g O₂/m²/day for Pena Blanca Lake, and Hallock and Ziebell (1970) indicated an average of 7.0 g O₂/m²/day for polluted waters. McConnell's study included production from submerged vascular plants, whereas Hallock and Ziebell worked in waters containing no rooted plants. It is apparent that algae and submergent vascular plants at Imperial Reservoir are sufficiently productive to make these waters comparable to other aquatic systems in the area.

The gross primary productivity data presented above were converted to a net production estimate of 0.73 kg/m²/year ash-free dry weight, which is an estimate of the production of the entire submerged community. Since a separate estimate was made for Najas, it may be subtracted from the estimate of net production of the entire submerged community to give a net production estimate of 0.29 kg/m²/year ash-free dry weight for planktonic and benthic algae alone (Table 1).

Allochthonous Energy Sources

In many open and semi-open systems, allochthonous energy contributions are extremely important (Teal, 1957; Nelson and Scott,

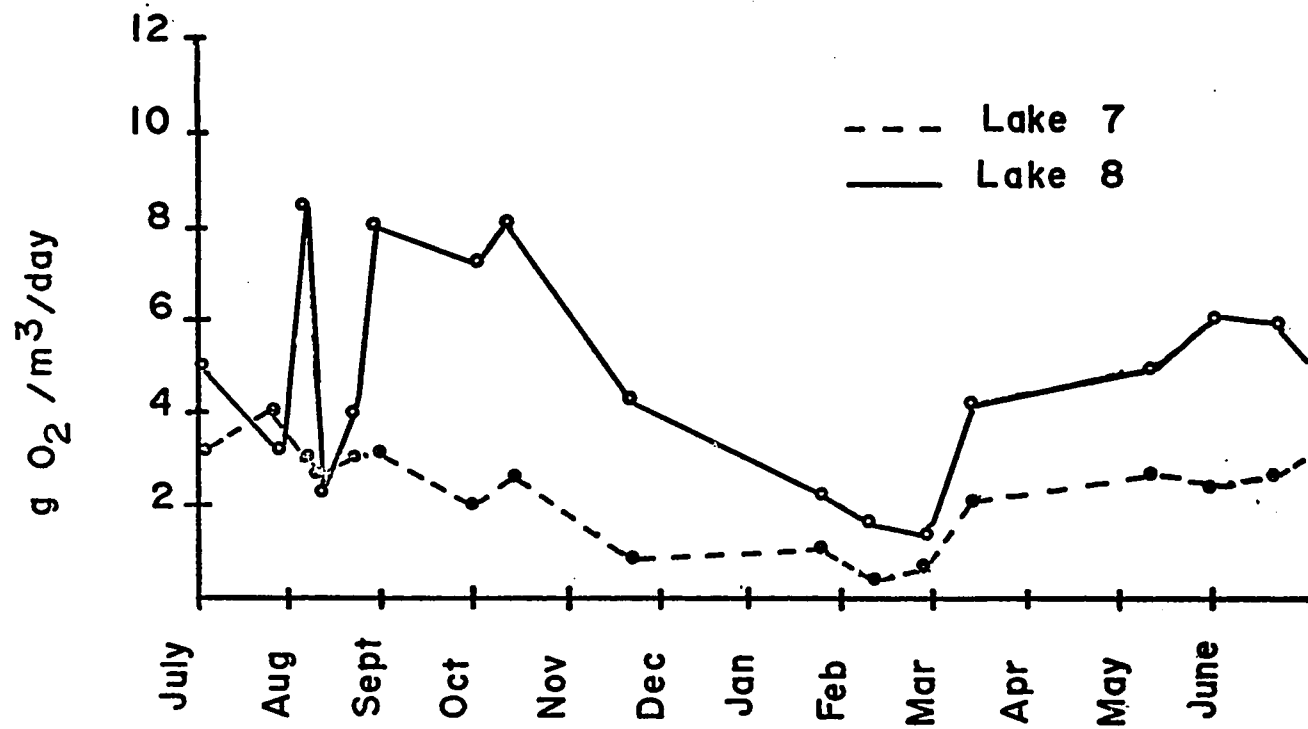


Figure 3. Gross primary production in two lakes (lakes 7 and 8) of contrasting morphology

1962; Hynes, 1963; Minshall, 1967; Fisher and Likens, 1972). Samples taken above, below, and at several points within the reservoir indicate that the marsh receives no more allochthonous material than it releases and that the total amount of allochthonous material is small. Allochthonous contributions are of minor importance to the lakes individually and to the reservoir as a whole.

Seston in the main river channel, at the lower end of the reservoir, averaged 0.055 g/m^3 (Fig. 4). A minor channel which received water that had passed through an extensive Typha bed averaged only 0.0025 g/m^3 . Seston entering this channel is similar to that entering most of the lakes within Imperial Reservoir.

That Typha beds are effective in precipitating seston from the river water is demonstrated by net seston quantities approximately 22 times greater in the main river than in the backwaters. The precipitation is a result of the slowing of the water causing the suspended particles to drop in the Typha beds. The drifting particles in the backwaters and connecting channels were of different types and origins than those in the river water. The particulate material in the river water was mostly Potamogeton filiformae (a vascular aquatic plant), terrestrial detritus, Typha detritus, and some zooplankton. In the open backwaters, the particles were mainly benthic algae, with a little zooplankton and Typha detritus.

A thorough study for evaluating seston within the study area was to be initiated only if preliminary work indicated that a large amount (over 10%) of the total energy in the open backwaters came from

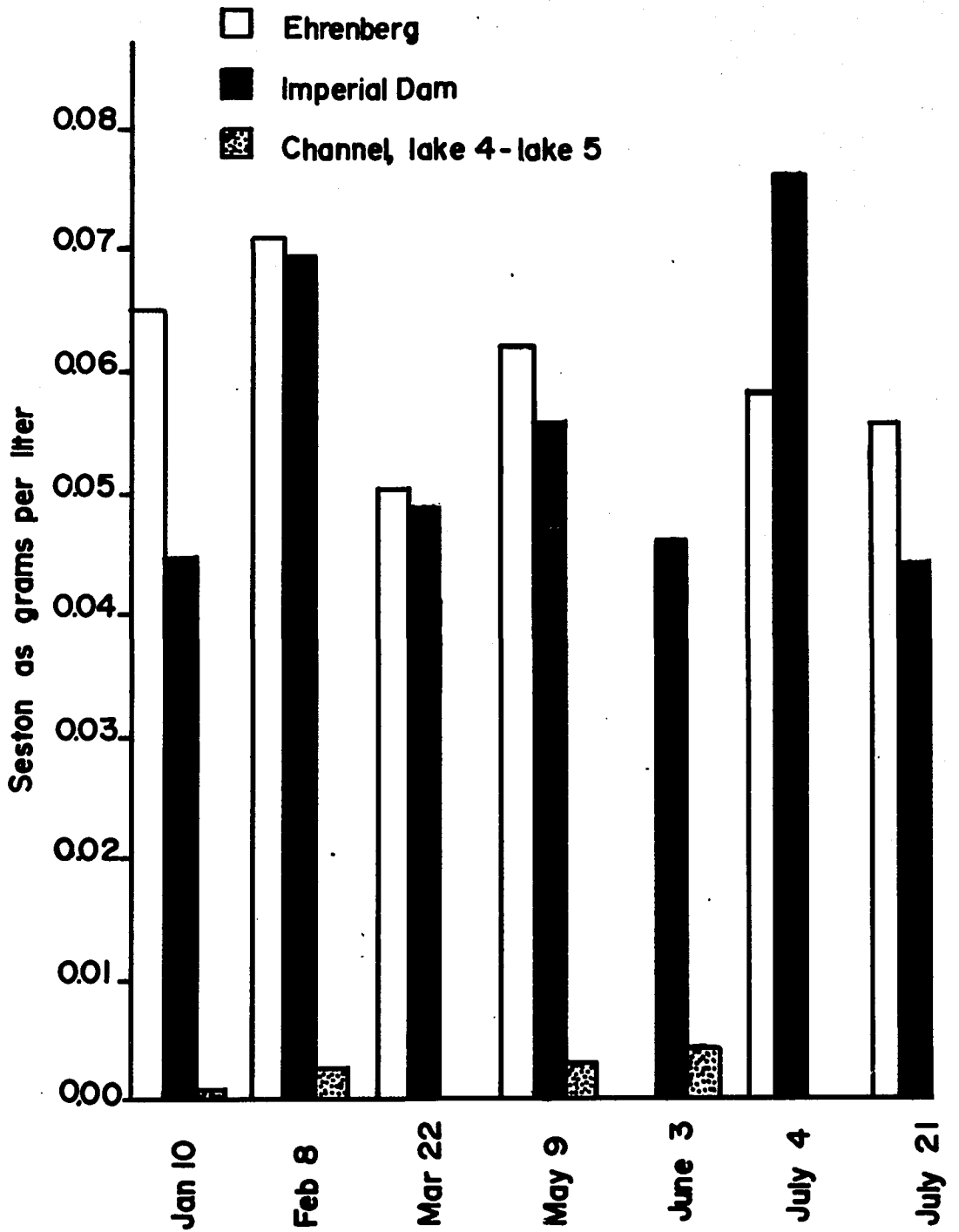


Figure 4. Seston above (at Ehrenberg), below (at Imperial Dam), and in a minor channel within Imperial Reservoir

allochthonous energy sources. These results indicated that no further evaluation of seston as an energy source was warranted.

Dissolved organic substances moving into the reservoir could also represent a source of allochthonous energy. Analysis for total dissolved organic material indicated that the reservoir gained no more oxidizable energy sources from the river than was lost downstream (Fig. 5). Lind (1971) found a similar situation in Lake Waco, Texas.

Infrequent flash floods could contribute both dissolved and particulate organic material from desert washes, but vegetation is sparse in the area surrounding the reservoir and the rains are very infrequent. When one such flood entered lake 3 (the only such occurrence noted in the course of the study), the pH dropped 0.2 units, presumably a result of incoming organic matter, since the pH change persisted for some time after the water cleared. Allochthonous contributions appear to be unimportant to the aquatic community of Imperial Reservoir.

Energy Contribution of Typha to the Sport Fishery

Typha is not used directly by any of the fishes in Imperial Reservoir. Only the breakdown products of Typha pass through the fish food web. The breakdown products of Typha are in the form of detritus and dissolved organics. These products were studied by determining (1) the distribution of Typha detritus (primarily blades), (2) the decomposition rate of Typha detritus, (3) the use of Typha detritus by benthic invertebrates, and (4) which of the organisms that derive energy from Typha are eaten by fishes.

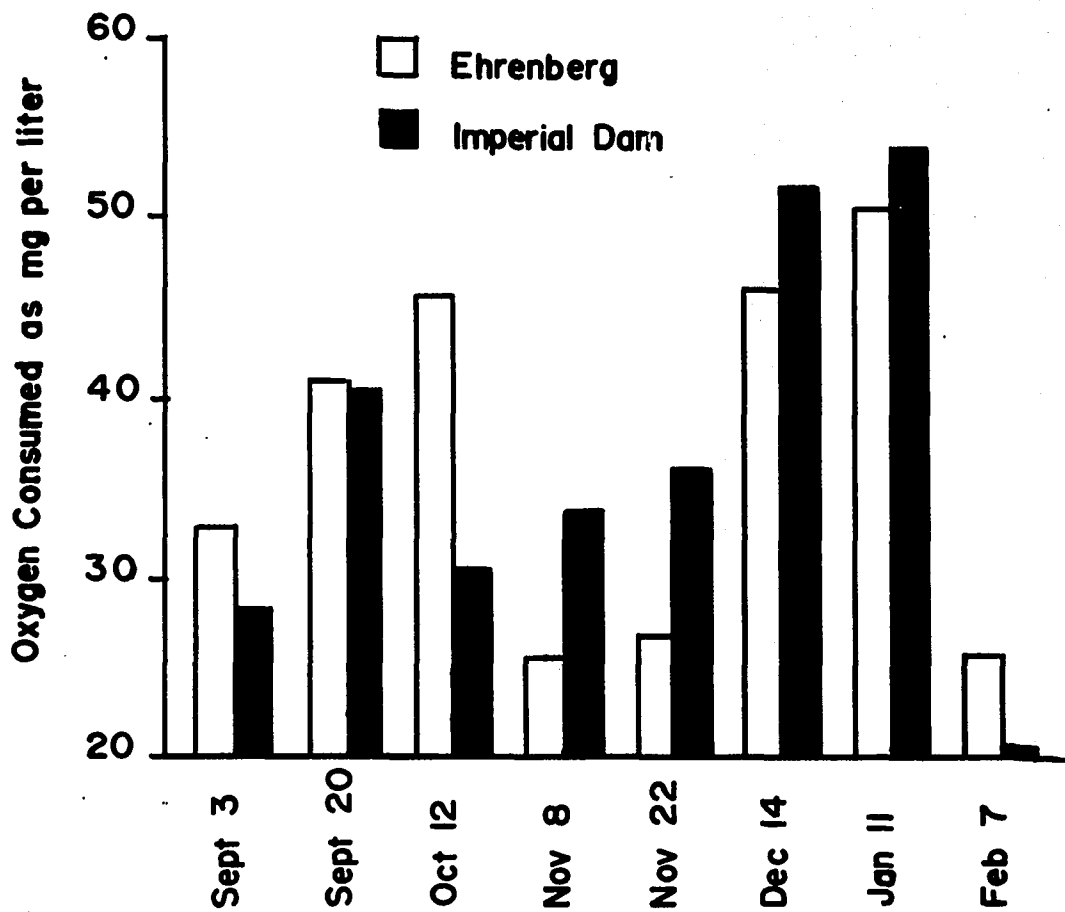


Figure 5. Total dissolved organic material above (at Ehrenberg) and below (at Imperial Dam) the reservoir

Since most of the sport fishes at Imperial Reservoir are carnivores, the following indirect efforts were made to evaluate the energy contributions of Typha to the fishery.

Distribution of Typha Detritus

Grazing on Typha blades was of minor importance. Aquatic mammals, cattle, and unidentified insects are known to utilize standing blades to a small extent, but most blades die, fall through wind action (Fig. 2), and decompose through the activities of various bacteria, fungi, and detritus-feeding organisms, thus becoming the base of detrital food chains.

Dredge samples indicate that most detritus is retained in or within a few meters of Typha beds (Fig. 6). The data from a series of litter-bucket transects in similar areas support this observation (Figs. 7 and 8). The proportion of organic material was slightly higher (2% to 3%) in the bucket samples than in the dredge samples from the same area. This was expected since the material in the buckets was less than 6 months old, while the dredge samples included sediments from previous seasons. Transects in lake 7 (where there was a paucity of emergent vegetation) were not substantially different from those in the open water of lake 4 (Figs. 7 and 8). These data indicate that no appreciable contribution was made by Typha detritus to the bottom of adjacent open-water areas.

In the lakes of Imperial Reservoir, at most water levels, slow (usually less than 10 cm/sec) currents pass through the Typha beds, but rarely are they of sufficient force to influence the distribution of

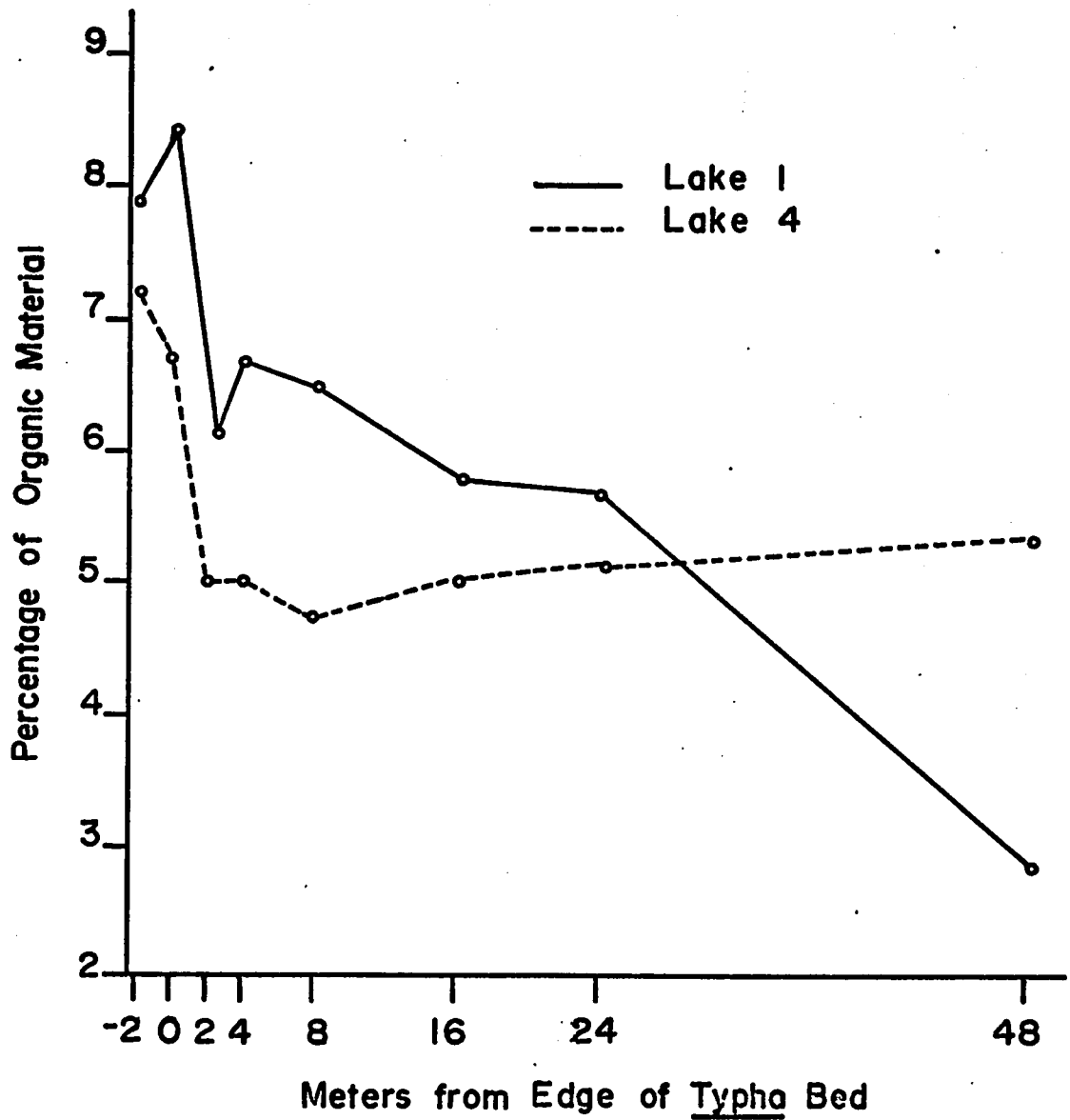


Figure 6. Percentage of organic material in the sediments in and near Typha beds in lakes 1 and 4

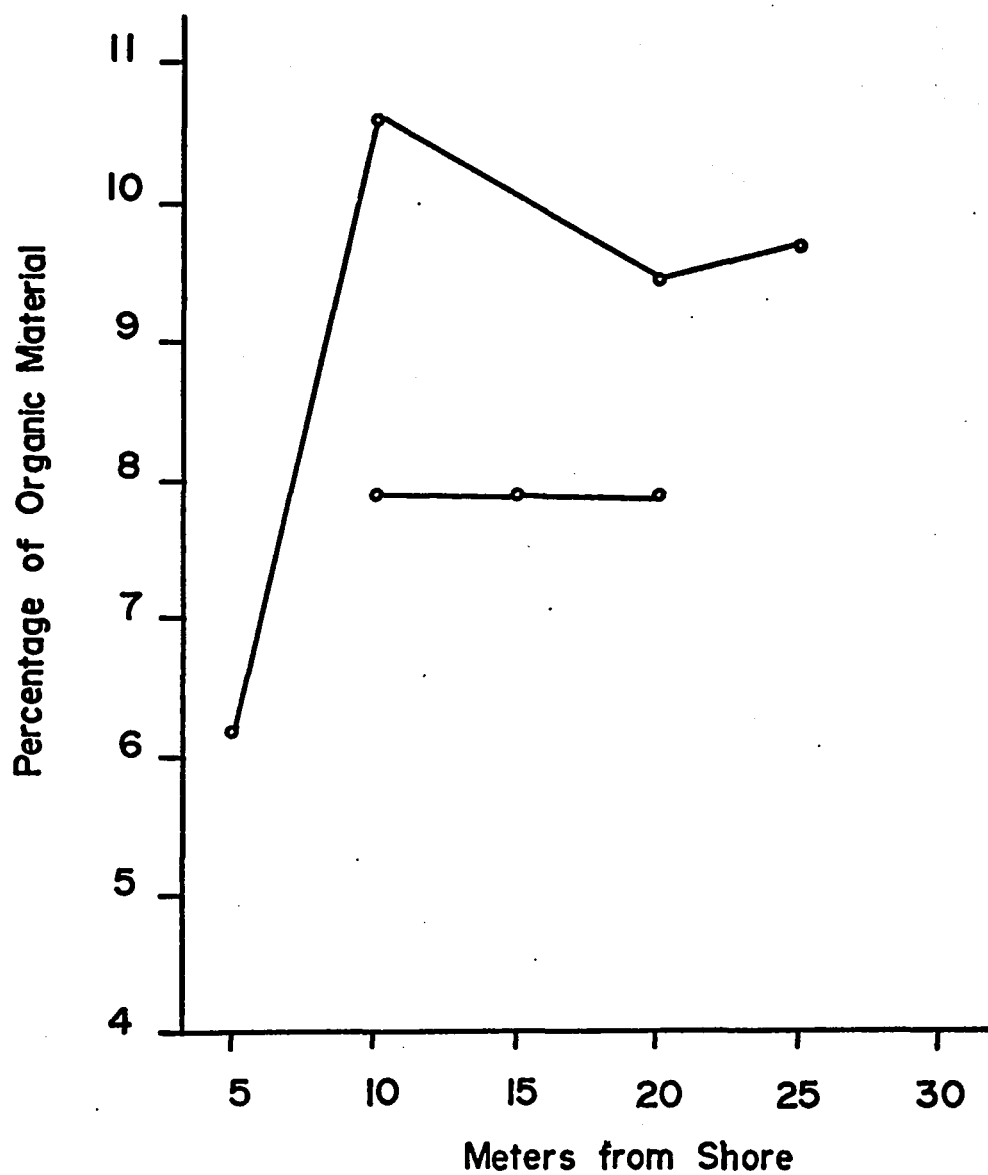


Figure 7. Percentage of organic material from two litter-bucket transects in lake 7

Transects were in operation from June until December, 1970.

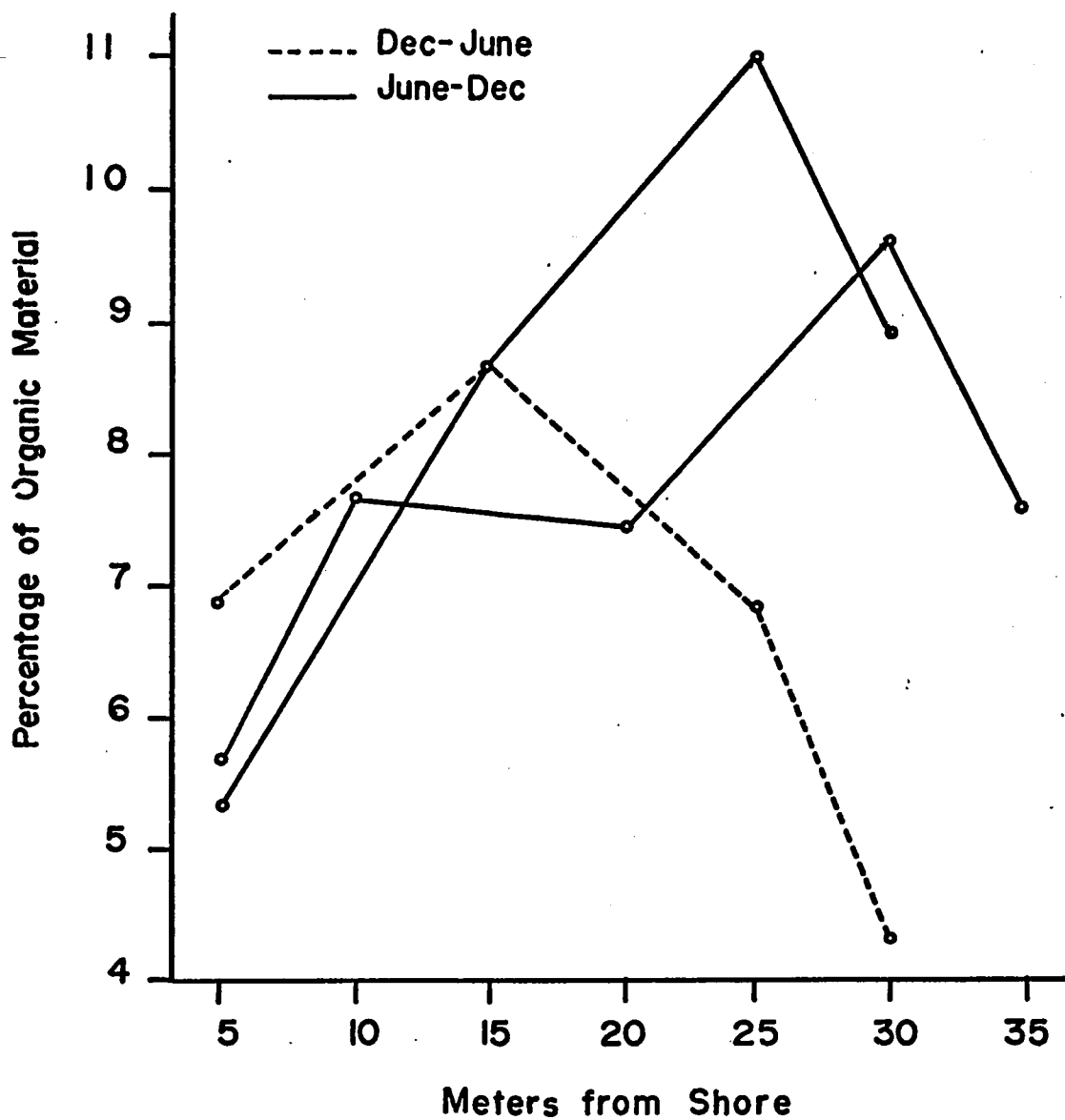


Figure 8. Percentage of organic material from three litter-bucket transects in lake 4

detritus. As the detritus studies above show, very little Typha detritus was carried out of the beds. Similar quantities of organic material were found in deposits of a lake with essentially no Typha and 10 meters out from an extensive Typha bed.

The lack of difference in type or quantity of particulate material in water entering and leaving the reservoir further supports the contention that most of the energy fixed by Typha beds is retained in or near these beds. Most of the material synthesized in the Typha beds along the lower Colorado River is retained in place.

Decomposition of Typha Detritus

Measurement of the total weight loss of blades is a common method for determining decomposition rates in marsh situations (Burkholder and Bornside, 1957; Odum and de la Cruz, 1967; Kormondy, 1968; Boyd, 1970a). The weight loss method was not practical to use in Imperial Reservoir because the large mesh size required in the litter bags caused the loss of particles of Typha and permitted silt to deposit in the bags. The rate of decomposition was determined by measuring the rate of fiber breakdown and the increase of organisms causing decomposition, through a nitrogen analysis method.

Analysis of crude fiber of Typha blades retained in litter bags indicated that bacterial decomposition was continuous throughout the year but differed in extent in the Typha bed and along the rocky shoreline. Crude fiber content of blade samples taken along the rocky shores decreased from 43% to 40% in one year, but fiber content in samples from a Typha bed decreased from 43% to 32% in the same period (Fig. 9).

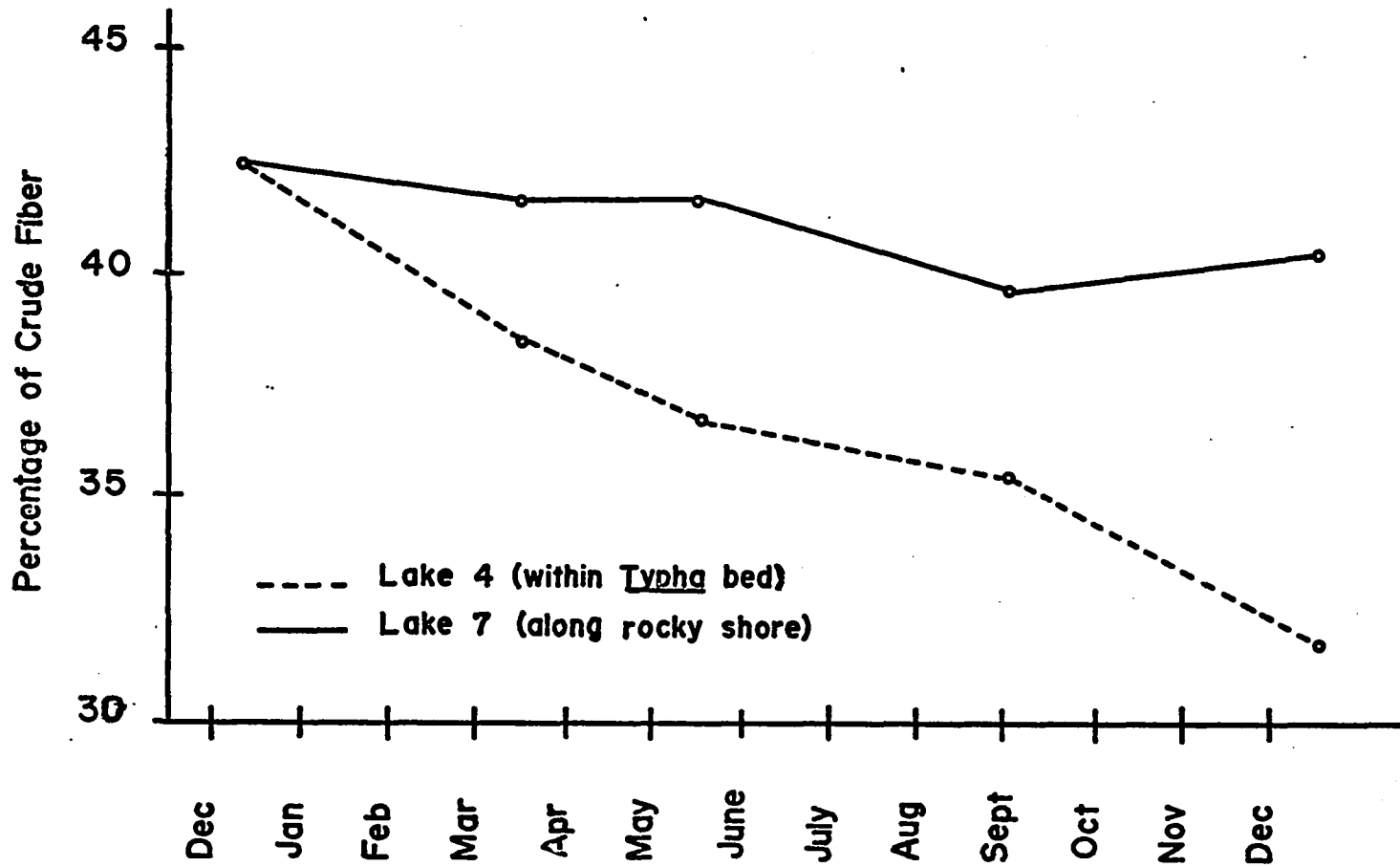


Figure 9. Mean crude fiber content of *Typha* blades submerged for varying periods in Fiberglass litter bags

Even after a year in the Typha bed, decomposition was only partially complete and all the original pieces of blade were still recognizable. In the Typha bed of lake 4, crude fiber analysis showed a 25% breakdown in the first year. Less than 10% of the fiber was broken down in lake 7. These findings are in general agreement with Boyd (1970a), who found that the total weight loss for Typha in litter bags was about 50%, most of which was accounted for by losses of soluble organic and inorganic material and small particles which passed out of the bags. Both analyses and visual observation indicate that decomposition is faster in the dense Typha environment than in the open-water areas.

Nitrogen analysis of litter-bag material indicates that the protein content was similar in samples from both lakes with a slight increase (from 4.75% to 8%) 12 months later (Fig. 10). This increase can be attributed to an increase in the population of organisms of decomposition. The protein content was slightly higher in the Typha beds of lake 4, probably a result of the faster decomposition there.

A substantial proportion of the energy aquatic plants contribute to marshes is in the form of dissolved organics. To demonstrate bacterial utilization of these compounds, extraction studies were made and compared with field sampling in and away from a large Typha bed. Extraction studies were designed to simulate the average amount of detrital input expected during periods of low water and stagnation within the Typha beds. Extractions of new Typha blade material indicate that at least 3.5% of the blade is readily soluble phenolic compounds and at least 4% is soluble carbohydrates. These data are from 1- and 6-day extractions, respectively, and are assumed to underestimate the

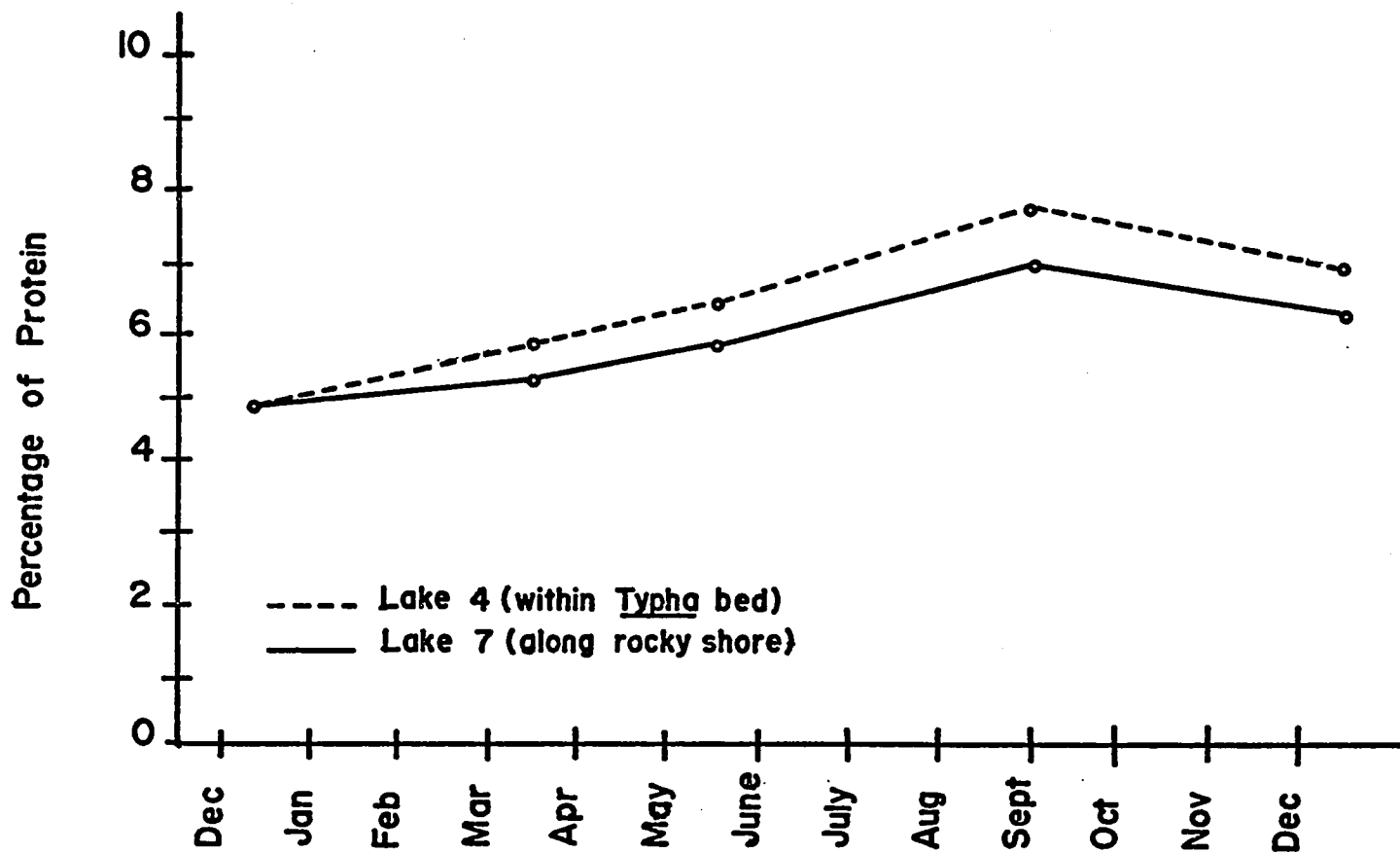


Figure 10. Mean protein content of Typha blades submerged for varying periods in Fiberglas litter bags

proportion of the Typha blades available as dissolved organic material, since blades fall throughout the year and contribute dissolved organics for some time after falling. At periods of stagnation within the Typha beds, the expected concentration of dissolved phenolic compounds and carbohydrates would be at least 1.0 and 1.2 mg/l, respectively. The continuing fall of blades may allow concentrations in excess of those expected.

On November 22 and December 14, 1969, relatively low water was observed in the reservoir. The sampling site in the center of a large Typha bed adjacent to lake 4 appeared to have standing or very slowly moving water. In field samples within the Typha beds on the above dates, concentrations of phenolic compounds were near 0.5 mg/l, which approached expected levels, while carbohydrate levels, near 0.5 mg/l, were lower than normal (Table 2). It is assumed that on these dates the organic matter concentrations in the water could have approached maximum levels. However, while phenolic levels were in fact raised, carbohydrate levels were lower than usually recorded. Apparently stagnation allowed the accumulation of phenolics, which are difficult for bacteria to break down, but not of carbohydrates, which are readily digested by bacteria.

Utilization of Typha Detritus by Invertebrates and Fishes

Typha may enter aquatic food chains by three routes: (1) it may be eaten directly, (2) it may be utilized as detritus, and (3) it may enter dissolved organic pathways. Little grazing occurs on standing Typha

shoots. Most blades fall and decompose annually, forming a large quantity of detritus.

Since it was not practical to quantify direct utilization of Typha detritus, only qualitative observations were made. The major macroorganisms abundant in Typha detritus are snails (Physa sp.), Asian clams (Corbicula fluminea), and midge larvae (Chironomidae). Midge larvae are the predominant benthic form both in Typha beds and in open water. When the stomach contents of midge larvae were microscopically compared to prepared cuticle samples of major angiosperms of the area, larvae taken in Typha beds were found to have ingested Typha detritus, whereas those taken in the open water of lake 7 contained no Typha detritus. Midge larvae apparently feed on all detritus, as they contained diatoms, algae, Typha, and other unidentified material.

Hundreds of snails and dozens of clams found in the litter bags had grown to twice the mesh size of the bags, indicating that they either utilized the Typha directly or fed upon bacteria that did. Physa, being scum feeders, probably fed upon bacteria and ingested only minute Typha particles loose on the surface of the detritus.

One dozen clams, 2 to 4 cm across, were taken from a Typha bed and a like number from an open-water area. Clams are filter feeders, and their stomachs contained such fine particles of organic detritus that microscopic comparison with the slides of prepared cuticular material was impossible. The variety of particles suggested that the clams ingest anything small enough, but only diatoms were recognizable. The ratio of diatoms to unidentifiable material in stomachs of clams was lower in

those from Typha beds. Where Typha detritus is abundant, it was ingested freely.

Typha contributes to a detritus food chain leading to the fishery. Distribution studies have shown that Typha detritus is abundant in the Typha open-water ecotone, as are invertebrates thought to utilize Typha detritus directly or indirectly. This ecotone was considered the most important nursery area for juvenile fish by Weaver (1971), and it was also an important feeding area for larger sport fish. Stomach samples from five sport fish species collected from this ecotone commonly contained clams, snails, and midge larvae, indicating that all were important food items for these fish (Table 3).

Use of Typha as Protective Cover by Fishes

A sonic tagging study was conducted during the summer and fall of 1971 to evaluate the use of Typha as protective cover by largemouth bass. Tagged bass were initially located 63 times during the study (Table 4). The greatest portion, 43% of these initial findings, were along or within Typha beds. On these occasions, 67 hours of tracking time were accumulated. Of this time, 36% was within or along Typha beds. When either initial findings or time are considered, Typha was the preferred habitat, with Najas, dead trees, and rocks as progressively less favored choices. Since Typha blades contain gas spaces that effectively block sonic transmission, fish were frequently lost when they entered the Typha beds. Thus the data collected underestimate the time spent in Typha marshes and consequently the importance of Typha. During this study numerous untagged largemouth bass and other

Table 3. Frequency of occurrence of food items in the stomachs of sport fishes from Imperial Reservoir
(Number of fish examined is in parentheses.)

Food Item	Number of Fish Containing Each Food Item				
	Largemouth Bass (13)	Redear Sunfish (13)	Bluegill Sunfish (14)	Channel Catfish (6)	Carp (6)
Benthic algae		x	xxxx	xxxxx	
Pterophyta					
<u>Typha</u>	x	xx			xxx
<u>Potamogeton</u>		x	x		
<u>Najas</u>		x	xxxxx xxxxxx x		x
Mollusca					
<u>Physa</u>	xxx	xxxxx x	xxxxx xxxxx		x
<u>Corbicula</u>		xxxxx xxxxxx	xxxxx xx		x
Crustacea					
Crayfish	x				
Insecta					
Tipulidae				x	
Chironomidae	xxx	xxxx	xxxxx		xxxx
Anisoptera	xxxxx	x	x		
Zygoptera		x	xxxx		
Vellidae		x	x		
Dytiscidae		xxx	x		
Limnephilidae			xxx		
Osteichthyes	xxxx	x	x		
Detritus	x		xxx		xxxxxx x
Empty	xx			x	

Table 4. Number of observations and hours of tracking time of three largemouth bass

Habitat	"Jack"		"Chuck"		"Bad Mouth"	
	Times Found	Hours	Times Found	Hours	Times Found	Hours
<u>Typha</u>	6	6.85	4	4.0	18	24.45
<u>Najas</u>	17	16.15	6	7.35	1	0.1
Submerged trees			10	8.10		
Rocks	1	0.5				

centrarchid game fish were observed along the Typha ecotone and in small ponds within the Typha beds. Bass and, presumably, other centrarchid game fish moved freely through the Typha beds from one lake to another when the water level was sufficiently high.

During this study each bass maintained two or three areas that might be considered territories. These territories were composed of specific sites along Typha and Najas beds, rocks, and dead trees, which were used interchangeably. Residence was for periods ranging from a few hours to more than 2 weeks. Bass were rarely found away from these favored areas, and when they were, they were generally moving continuously. The greatest distance covered was about 600 meters. Fish showed no hesitation about entering murky major channels to re-enter other lakes. Thunderstorms and darkness did not alter the normal activities of the fish studied.

Limnological Measurements

Water temperatures and mean monthly air temperatures for Imperial Reservoir are shown in Table 5. The water temperature reached a maximum of 32.2°C (90°F) in August, a minimum of 7.8°C (46°F) in January, and followed the mean air temperature throughout the year. No permanent stratification was noted within the reservoir. Larger Typha beds were found to affect water temperatures. Shading in a Typha bed approximately 140 meters wide and with a current of less than 10 cm/sec, cooled the water from 1 to 1.5°C at midday during spring months. This cooling influenced spawning of the centrarchid fishes present. No spawning was observed below this bed and a similar bed in another lake.

Alkalinity, as CaCO₃, ranged between 135 and 165 mg/l, and the pH was generally between 7.8 and 8.0 at most points in the reservoir (Table 5). Conductivity tended to increase in the more isolated backwaters, where values near 1,800 micromhos/cm were frequently obtained. Conductivity in lakes not connected to the river reached 40,000 micromhos/cm. In the river more typical values of 1,000 to 1,400 micromhos/cm were found.

Light penetration was measured at midday at the bottom of lakes 7 and 8 in conjunction with the gross primary productivity study (Table 6). Light intensity at the bottom of the relatively shallow lake 8 was generally eight times greater than that in lake 7, but at no time could the benthos be considered to be below the euphotic zone.

Table 5. Mean monthly air temperature, water temperature, and pH for Imperial Reservoir

Date	Temperature				pH
	Air		Water		
	°F ^a	°C	°F	°C	
<u>1969</u>					
Sept.	89.7	32.1	84.2	29.0	7.8
Oct.	71.9	22.15	66.9	19.4	7.9
Nov.	64.3	17.95	51.8	11.0	8.0
Dec.	56.0	13.35	51.8	11.0	8.0
<u>1970</u>					
Jan.	54.4	12.45	46	7.8	8.1
Feb.	61.4	16.35	55	12.8	8.1
Mar.	62.5	16.95	63	17.2	8.1
Apr.	66.1	18.95	64	17.8	8.1
May	80.3	26.85	75	23.9	8.1
June	87.3	30.70	80	26.65	8.0
July	95.1	33.05	86	30.0	7.9
Aug.	94.2	34.55	87	30.55	7.7

a. Data from U.S. Department of Commerce, Weather Bureau (1970).

Table 6. Light penetration as a percentage of incident illuminance at the bottom of lakes 7 and 8 at midday

Date	% Illuminance at Bottom	
	Lake 7	Lake 8
July 27	4	47
Aug. 11	5	40
Nov. 19	20	65
Jan. 25	12	75
Feb. 26	7	58
Mar. 31	3	60
June 1	8	62
June 19	4	40

DISCUSSION

The intent of this discussion is to consider some of the relationships between emergent plants and the rest of the freshwater community. Data collected in this study indicate that Typha and other emergent plants contribute to aquatic communities in two major ways: (1) their photosynthetic activities contribute fixed energy and (2) their physical presence influences both the morphology of the open-water areas and the variety of associated organisms.

Typha as Food

Emergent plants are one of four potentially important energy contributors in the aquatic community of the study area. Submergent vascular plants, algae, and allochthonous material have been shown to be, pro rata, less productive than emergent plants (Typha). Typha production is more than twice as great as that of all other components combined. This is not surprising, since Typha has the advantages both of aquatic plants with unlimited water and of terrestrial plants with abundant available CO₂ and soil nutrients, as well as long (3 to 5 meters) blades well suited to intercepting light energy. As mentioned previously, Typha covers an estimated 60% of the vegetated shorelines in the lakes studied and approximately one-third of the entire surface area of the reservoir. Thus it is estimated that the Typha beds produce well over two-thirds of the total fixed energy (biomass) within the backwaters of the reservoir.

Although Typha beds are the largest energy fixing component in the reservoir, they are not necessarily the most important component of the ecosystem. Typha, like other emergent hydrophytes, has a high proportion (greater than 40%) of fibrous material that is not easily broken down in nature. Consequently, much of the energy fixed in Typha blades is not directly available to grazing organisms but may be utilized only through detrital food chains.

Detrital Food Chains

Detrital food chains are a major link between autotrophs and some larger consumers as established by Odum (1957), Smirnov (1958), Teal (1962), Odum and de la Cruz (1963, 1967), Phillipson (1966), and Teal and Teal (1969). The great importance of detritus in tropical fisheries was discussed by Hickling (1961). Odum and Smalley (1959) have discussed energy flow based on the detritus of Spartina alterniflora in a salt marsh. Darnell (1958) documents the importance of detritus in the diet of many fish and macroinvertebrates in a Louisiana estuary. The contribution of detritus in lotic environments has been discussed by numerous authors (Nelson and Scott, 1962; Hynes, 1963; Egglshaw, 1964; Minshall, 1967; Kaushik and Hynes, 1968; Fisher and Likens, 1972).

Most of the detrital food chains discussed in the above studies were facilitated by strong water movements. Emergent plants, such as Spartina, frequently form the base of important food chains in estuaries with cycling water movements. In estuaries, where detritus is transported by tidal action, it is available as an energy source in areas far

from the producing plant communities (Darnell, 1958; Heald, 1969; Teal and Teal, 1969).

The strong water movements which in estuaries facilitate the dispersion of detritus and the establishment of detrital food chains are absent in Imperial Reservoir. Imperial Reservoir is one of an extensive series of reservoirs along the lower Colorado River which have effectively eliminated flooding. Water levels change slowly, and the extremes vary only about 0.5 meter. Changes of this magnitude are insufficient to move appreciable amounts of detritus out of the Typha beds. Rare flash floods from desert washes may temporarily disrupt the stability in some areas.

Studies on the distribution of Typha detritus indicated that the vast majority was retained in or near the Typha beds (Figs. 6, 7, and 8). Lack of water movement has prevented Typha detritus from reaching the open-water communities within the reservoir. It is available only to the organisms in or within a few meters of the beds. Consequently, the extensive detrital food chains which might be predicted from the high Typha productivity rates have not been developed, and the system is much less efficient than those in estuaries. Detrital food chains based on Typha have been established only in the Typha open-water ecotone and within the Typha beds. This ecotone was considered the most important nursery area for juvenile fish by Weaver (1971). Larger fish are commonly found in this area, which is an important feeding area as is indicated by the relatively low invertebrate populations (Hayne and Ball, 1956). The stable water levels and slow water movements which

encouraged the growth of the Typha beds have limited their contribution to the reservoir.

Decomposition of Typha

Decomposition of Typha detritus is slow. Crude fiber analysis revealed that under the conditions of the study, the most rapid fiber breakdown was about 25% in the first year. This rate was achieved only in litter bags suspended within a Typha bed. Both analysis and visual observation indicate that decomposition of Typha is faster in situ than in other areas. No measurable differences in water quality were found between the two areas. The best explanation for this difference in decomposition rates is that abundant supplies of bacteria with an ability to decompose Typha were present in the presence of a plentiful supply of their substrate (Burkholder and Bornside, 1957).

In estuarine situations, macroorganisms, usually crustaceans, are present which in their foraging activities aid and accelerate detritus formation by physically shredding the particles. When in smaller particles, the detritus has more surface area exposed to bacterial attack and consequently is enriched with the bacteria, as is measurable by an increase in the protein content of the detritus. This enrichment was observed in the litter-bag studies, where the protein content of the Typha blades increased from 4.75% to nearly 8% as the blades were slowly decomposed. Presumably this process would have been accelerated if suitable macroorganisms had not to a large degree been excluded. The activities of small snails and clams may have slightly increased the decomposition rate.

When the detritus particles composed of structural carbohydrates and bacteria are ingested by detritus feeders, the bacteria are used as food while the particle is often reduced in size before being excreted. This process is cyclical as the smaller particles are again attacked by bacteria, and the particle size progressively decreases (Heald, 1969). Particle breakdown progresses until the particles reach colloidal size, with an associated increase in nitrogen content resulting from bacterial increase. The result is a relatively protein-rich food source readily utilized by suspension feeders (Freedon, 1960; Jorgensen, 1966; Heald, 1969). Suspension feeders, such as Corbicula and various zooplankton exist in large numbers within the reservoir. Typha beds may contribute substantially to the energy flow of the reservoir through this pathway, since colloidal particles may be easily distributed throughout the reservoir by the slow currents present. A system involving transport of particles of colloidal size only is less efficient of energy than estuarine systems in which larger fragments are also transported.

At Imperial Reservoir, the two common macroorganisms that help fragment Typha detritus and accelerate the formation of colloidal-size particles are carp (Cyprinus carpio) and chironomid midge larvae. These organisms, which are able to utilize relatively large fragments of Typha with its associated biota as food, represent links in the detrital food chain which have their counterparts in estuarine systems (Darnell, 1958; Heald, 1969; and Teal and Teal, 1969). These are, however, the only detritivores found in large numbers at Imperial Reservoir. Their distribution within the Typha beds is not regular, and their influence on the

physical reduction of Typha detritus is mainly limited to deeper water areas within the Typha beds and to the ecotone.

Dissolved Organic Material

Dissolved substances from Typha beds may enter the food chain of the open-water community directly or indirectly through bacterial complexes. The rapid disappearance of dissolved carbohydrate in the Typha beds has already been mentioned. The direct use of dissolved carbohydrates by suspension-feeding organisms, such as molluscs, has been noted by Collier (1959). Gorbunov (1946), Warren et al. (1964), and Jorgensen (1966) have thoroughly documented the ability of bacteria to take up dissolved organic material. Adams (1970) has demonstrated that the addition of carbohydrates resulted in increased bacterial numbers. Bacteria consumed by larger organisms can form an important link in the food chain leading to the fishery. Larvae of Aedes aegypti (a mosquito) were raised on purely synthetic diets by Singh and Brown (1957), but their growth was greatly enhanced in cultures that were contaminated with bacteria. Freedon (1960) has shown that black fly (Simulium articum) larvae are able to utilize bacteria as food. McConnell (1968), one of the few investigators to have considered dissolved organic contributions of recently produced detritus, found oak leaf extracts useful as an energy source to microorganisms and consequently to filter-feeding Xenopus leavis (an African frog) and Physa (snails). Gorbunov (1946) and Warren et al. (1964) have shown that the addition of organic material resulted in increases in both bacterial and fish production.

The decrease in phenolic levels as water passed slowly from the Typha beds into open water, although slower than that of

carbohydrates, could simply be a dilution effect, but it more likely also results from bacterial breakdown, since phenolic compounds are broken down more slowly than carbohydrates.

The data from the present study indicate that bacterial uptake of dissolved organics probably occurs. Extraction studies indicate that something in excess of 7% of the annual shoot production, or more than 130 g/m²/year, should be available as dissolved carbohydrate and phenolic compounds. These compounds are available for uptake by bacteria, which are available to suspension-feeding organisms. With the presence of suspension-feeding organisms (clams and zooplankton) it is reasonable to assume that dissolved organics are contributing to the various food chains in Imperial Reservoir.

Carbohydrates and possibly phenolic compounds liberated from Typha detritus may also enter aquatic food chains through heterotrophic algae. Presumably the same is true for Najas. Lewin (1962) and Adams (1970) suggested that this is possible in warm waters as are characteristic of Imperial Reservoir. Adams (1970) has demonstrated significant increases in algal biomass resulting from the addition of carbohydrate. Similarly, Wetzel (1969) showed that periphytic algae may heterotrophically utilize dissolved organic compounds liberated from their substrates, the aquatic macrophytes.

Relative Importance of Typha as a Food Source

Typha contributes energy to the fishery through several pathways. This energy contribution, although difficult to quantify, is probably very important to fishery production at Imperial Reservoir. Although Typha is the dominant primary producer in the study area and is available as an energy source throughout the aquatic community, the efficiency of energy transfer is relatively low.

A factor which may minimize the importance of Typha as an energy source is its nutritive quality. Although the caloric content of emergent and submergent aquatic macrophytes is nearly constant on an ash-free dry weight basis (Boyd and Goodyear, 1971), the ratio of structural to nonstructural carbohydrate influences the availability of energy to herbivores and decomposers. Typha blades, which are almost half crude fiber, were only 25% decomposed after one year. Najas foliage, which has very little structural carbohydrate, was almost completely decomposed after 6 months. The difference in fiber content results from the difference in support requirements; submergent species in relatively still waters require minimal supporting structures.

The presence of fewer structural carbohydrates is frequently associated with an increased proportion of more readily available components, including protein. There is a marked difference in the protein content of Typha blades and Najas foliage. The protein content of new Typha blades in this study was 4.75% in October. Boyd (1970b) found 4% protein in Typha and 14.4% in Najas guadalupensis, an approximately threefold difference. These figures are representative of protein differences between submergent and emergent species.

In 9 months of bacterial attack, the proportion of protein in Typha detritus increased to nearly 8% from its initial value of 4.75%. Thus, the nutritional quality was enhanced by the bacteria (Odum and de la Cruz, 1967; Kaushik and Hynes, 1968; Heald, 1969). Since Typha has a high proportion of structural carbohydrate and receives little grazing by herbivores, it is almost exclusively used by detritivores. Consequently, the initial nutritive value underestimates its relative importance.

The lower structural carbohydrate content of Najas allows it to enter detrital chains much more rapidly than Typha. It is also utilized directly by fish. Since Najas is more easily broken down, less energy is lost to bacterial metabolism. Consequently a greater proportion is available to detrital food chains.

The net production rate of Typha blades was more than four times that of Najas foliage. Since the two species occupy approximately equal portions of Imperial Reservoir, Typha would appear to contribute roughly four times as much energy as Najas. However, the readily available fraction of the Typha biomass is much smaller than that of the Najas. Thus the available food energy contributed by Najas is more important relative to that contributed by Typha than would be estimated from gross productivity data.

Typha as Game Fish Habitat

Energy contributions are but one of the important functions of Typha beds in the reservoir. Their presence can greatly influence the species composition and the distribution of coexistent organisms, and they influence the morphology of open-water areas as the reservoir fills naturally through eutrophication and siltation.

Shelter for large and small fish is an important function of many emergent plants (Bennett, 1962). The importance of Typha beds as habitat for fish has generally been assumed but rarely considered in the literature.

The use of Typha margins at Imperial Reservoir by juvenile fish was noted by Weaver (1971). For 6 to 8 weeks in the spring, Typha beds are the only major refuge for juvenile bass. Largemouth bass spawn in

April when water temperatures reach 60°F (15.5°C). Substantial numbers of juvenile bass would not survive if the Typha beds were not available for protective cover at this time. Najas, the only other important source of cover, is not in evidence until approximately the first of June. Other centrarchid game fish begin spawning in May at or just before the appearance of Najas beds, when the water temperature reaches about 70°F (21°C). This 6- to 8-week separation between spawning times of bass and other centrarchids results from a temperature plateau at approximately 65°F (18°C) that occurs annually within the reservoir.

It is this separation of spawning times that allows predator (largemouth bass) populations to maintain a balance with prey (other centrarchid game fish) populations at Imperial Reservoir. The juvenile bass may reach 8 cm by the first of June, when prey fishes spawn. The bass are then large enough to prey effectively on the smaller, more recently spawned fish. In most northern states a great deal of effort has been directed toward selecting suitable stocking ratios for warm-water game fish. In these areas, with longer pronounced winters, Typha beds are nearly obliterated by spring and are of little value as protective cover for juvenile fish. Almost invariably populations in these areas soon become unbalanced and the fisheries deteriorate.

Typha beds influence water temperatures, since in many places water slowly moves through them into the lakes. During the spring months, water was cooled 1 to 2°C as it passed through a bed approximately 150 meters wide. Cooled waters may form microenvironments within the reservoir that are both favorable and unfavorable to the fishery. No spawning was observed below the Typha bed studied nor below several

similar beds. The cooler waters were not favorable spawning sites for fish that initiate spawning upon warming trends. Temperatures in excess of 86°F (30°C), which cause respiratory difficulties in largemouth bass (Johnson and Charlton, 1960), were observed in open-water areas but not below the Typha bed studied. These beds could provide bass refuge during summer months.

A behavioral study with telemetry methods conducted during the summer of 1971 on big largemouth bass indicated that Typha beds were the preferred habitat in this reservoir. Bass moved freely through the beds at most water levels. At high water levels bass and other centrarchid game fish were frequently seen in small openings within large Typha beds. At all times, the Typha open-water ecotone was a preferred habitat for centrarchid game fish. Tagged bass in this study moved within relatively restricted areas in one or possibly two adjacent lakes, possibly as a result of extensive Typha beds. The greatest distance covered was probably not more than 600 meters. Rawstron (1966) found the average movement of tagged bass to be 0.7 mile (1.17 km) in Folsom Lake where water levels vary considerably and few emergents are present. Individual bass ranged as far as 4.5 miles (7.7 km) in Clear Lake, where emergent vegetation is restricted to isolated clumps (Kimsey, 1957).

Largemouth bass will not spawn on silt. They required suitable firm substrates, such as rocks, clean sand, gravel, and aquatic vegetation (Emig, 1966). Typha beds have served this purpose at Imperial Reservoir. Schools of juvenile largemouth bass were observed in isolated lake 8, where the bottom is entirely silt and the only suitable firm areas are the edges of the Typha beds. A stable substrate is essential for

abundant populations of various important forage organisms which require a firm substrate, including molluscs and some aquatic insects.

The extensive root systems of the Typha beds have contributed to the stabilization of the banks along many of the channels and along the margins of many lakes within the reservoir. Typha seeds require mud or very shallow water for germination, but once the plants are started, the rhizomes spread them into deeper water to approximately 0.5 meter. Within one season a single plant may cover an area 10 feet (3 meters) in diameter through rhizomatous reproduction (Yeo, 1964). Established Typha beds are able to maintain monospecific culture, possibly through the release of autotoxins (McNaughton, 1968).

Many of the beds studied are rapidly eliminating their own habitat by trapping sediments and depositing litter. They represent accelerated stages of eutrophication of the shallow areas of the reservoir. Within a year, a new sandbar can form and be colonized by Typha. Once established, a Typha bed can slow water flow from greater than 1 m/sec to less than 0.1 m/sec within a few meters. One such sandbar was covered with approximately 250 m² of Typha in one growing season. By the following spring, enough silt had been deposited that an island was formed, which was covered only at high water levels. Fiber from the blades and extensive root systems contributed to the formation of the island. The fiber and the root system help to maintain the island against the erosive forces of a major channel.

When Imperial Reservoir was completed, most of its calculated storage capacity had already been lost to siltation. The reservoir remains little more than a diversion dam with extensive shallow-water

areas. Since that time, the water has been maintained at a relatively constant level, varying by only a few feet. These conditions are ideal for emergent vegetation, such as Typha. Ironically, this reservoir, which was designed for water conservation and manipulation, has created a situation most favorable for Typha, which consumes remarkable quantities of water. Otis (1914) found that Typha beds can transpire up to three times the amount of water that evaporates from open-water surfaces under similar conditions. Central in plans for water conservation in the area is the elimination or reduction of these emergent communities and as many of the associated shallow-water areas as possible. The most obvious way to reduce emergent vegetation is to reduce the extent of shallow-water (less than 1 meter) areas. Aquatic primary production data from this study showed that lakes averaging 3 meters deep were more productive than those averaging only 1 meter. Gross primary productivity for lake 7 (about 3 meters deep) was $6.30 \text{ g O}_2/\text{m}^2/\text{day}$, while lake 8 (1 meter deep) was only $4.75 \text{ g O}_2/\text{m}^2/\text{day}$. This significant difference results from a more efficient utilization of light energy in the deeper water column. The bottom light intensity was generally eight times greater at the bottom of lake 8 than in lake 7, where light transmittance was generally less than 5%. When compared to the overwhelming production of the Typha beds, this difference in gross production is small.

A relatively shallow system with a large proportion of emergent vegetation is more favorable for a sport fishery than one with steep shores and water depths greater than 3 meters, both in terms of energy input and protective cover.

Although beyond the scope of this study, Typha beds are habitat for fur-bearing mammals and many shorebirds, including the endangered Yuma clapper rail (Rallus longirostris). The upper reaches of the reservoir are within the Imperial National Wildlife Refuge. The presence of these beds with their associated wildlife contributes immeasurably to the esthetic value of the reservoir.

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