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Spatial, Seasonal and Diel Distribution of Fishes in a California Reservoir Dominated by Native Fishes

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ABSTRACT

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During 21 months of sampling with various techniques, we captured 24 species of fish in Britton Reservoir. Nine species comprised over 96% of the number of fish captured and approximately 88% of the biomass. Five native non-game species accounted for over 77% of the catches.

The native non-game fishes have maintained large populations in the reservoir despite continued introductions of non-native species. Two sources of non-native species exist. The first is the introduction of exotic species directly into the reservoir during fish-stocking programs. The second is the continuous movement of non-native fishes into the reservoir from large populations which reside in a major tributary of the reservoir. Factors responsible for the large number of native fishes are: management of the reservoir for hydroelectric generation; temperature regime; reservoir morphology.

The fish community structure is stratified along two axes: upper basin/lower basin and inshore/offshore. Most of the 24 species were found inshore: 14 species were found offshore. Four of the native non-game fishes were most abundant in the upper basin: three introduced non-native fishes were most abundant in the lower basin of the reservoir. The offshore community was dynamic on a daily and seasonal basis.

INTRODUCTION

Reservoirs in California and the southwestern U.S.A. are typically dominated by introduced fishes such as common carp, *Cyprinus carpio* Linnaeus: catfishes (*Ictalurus* spp); centrarchid basses, *Micropterus* spp; and sunfishes (*Lepomis* spp). Usually these fishes have replaced the native stream fishes that initially colonize new reservoirs (Moyle, 1976, 1986). The mechanisms of re-

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placement are uncertain, but predation on native fishes by introduced piscivores, particularly centrarchid basses, is probably a major factor (Moyle et al., 1987). In a few reservoirs, the native fishes have retained their dominance, despite repeated introductions of other species. Such reservoirs are generally regarded as problems by fisheries management agencies because most of the native fishes such as suckers (*Catostomus* spp), squawfish (*Ptychocheilus* spp) and tui chubs, *Gila bicolor* (Girard), are of little interest to anglers. However, these reservoirs can act as refuges for declining populations of native fishes. This function assumes additional importance when the native fishes are a major source of food for the threatened bald eagle, *Haliaeetus leucocephalus* (Linnaeus).

In California, one of the reservoirs still dominated by native fishes is Britton Reservoir on the Pit River in the northeastern part of the state. This reservoir was created in 1925 to store water for hydroelectric power production. Because it is located in a popular tourist area, numerous attempts have been made to enhance its sport fishery through introductions of salmonid, centrarchid and ictalurid fishes. The introductions, however, have met with only limited success (California Department of Fish and Game, 1980). Non-quantitative surveys conducted by the California Department of Fish and Game (CDFG) indicated that the most abundant species were native species: Sacramento squawfish, *Ptychocheilus grandis* (Ayres); hardhead, *Mylopharodon conocephalus* (Baird and Girard); Sacramento sucker, *Catostomus occidentalis* (Ayrest); tule perch, *Hysterocarpus traski* (Gibbons). Adult hardhead, squawfish and sucker are relatively large and all can exceed 500-mm standard length. The principal game fishes were largemouth bass, *Micropterus salmoides* (Lacepède), and black crappie, *Pomoxis nigromaculatus* (Lesueur); another centrarchid, bluegill, *Lepomis macrochirus* (Rafinesque) was also present. Even though the fishery is regarded as poor in comparison with other Californian reservoirs, the native non-game fishes are abundant enough to form a forage base for the largest concentration of nesting bald eagles in California (Detrich, 1985) as well as nesting osprey, *Pandion haliaetus* (Linnaeus). In addition, the tule perch population is one of the few reservoir populations of this live-bearing fish (family Embiotocidae), as well as being the northern-most population (Moyle, 1976).

This study was designed to answer the following questions. (1) What is the composition of the Britton Reservoir fish community? (2) How do the various fish species use the habitats available in the reservoir? (3) How have the native non-game fishes retained their dominant status? (4) What characteristics of the native non-game fishes make them available as forage for eagles? To help answer the last question, simultaneous studies were conducted to determine the feeding habits of the local eagles (Hunt et al., 1989). The ultimate purpose of both studies was to find ways to improve the sport fishery without harming the bald eagles or significantly impairing the power-generating function of the reservoir (Dombeck et al., 1984).

STUDY AREA

Britton Reservoir is a forebay reservoir for hydroelectric generation (Pit 3 hydroelectric facility) located on the Pit River, in Shasta County in northern California. The Pit River is a major tributary to the Sacramento River system, draining much of northeastern California. Britton Reservoir was filled in 1925 and covers 520 ha. The reservoir is approximately 13 km long and in most places less than 1 km wide (mean width 0.4 km). The reservoir is relatively steep-sided and deep, with the exception of the upper portion and a few shallow coves. The reservoir is divided into two different habitats. The upper portion is more riverine (mean width 0.3 km, mean depth 9 m); the lower portion is more lacustrine (mean width 0.5 km, mean depth 16 m). Hat Creek, a major tributary with a stable flow of about 14 m^3 s^{-1}, enters Britton Reservoir at its upstream end. Burney Creek, another large tributary (4 m^3 s^{-1}), enters the south side of Britton Reservoir about 2 km from the dam. The Pit 3 hydroelectric facility is operated at a peaking mode during the portion of the year when the reservoir is not spilling, which is generally from May to late November or December. As part of the peaking mode of operation, the level of Britton Reservoir fluctuates with power demand, approximately 1–2 m on a weekly basis. However, the pattern is variable, particularly during very hot weather when demand for electricity is high. This peaking mode, coupled with a low retention time of the reservoir (6 days), limits the formation of a stable thermocline.

METHODS

Electrofishing

We electrofished at 27 stations (Fig. 1) on a monthly basis from March 1983 through February 1984 using a Colfelt, boat-mounted electrofisher generally set at 350 V.d.c. and 60 pulses s^{-1}. From March 1984 through July 1984 we suspended electrofishing to avoid biasing bald eagle feeding studies with fish killed by the electrofishing operation. (In preliminary studies we determined that electrofishing could cause a 25% mortality of Sacramento sucker, a major prey item of the bald eagles.) We resumed electrofishing in August 1984 and sampled through December 1984. The electrofishing stations were approximately 50 m in length. All sampling was conducted during daylight, except the stations in the upper portion of the reservoir which were sampled after sunset in August 1983. Each captured fish was measured (± 1 mm), and a selected number were weighed (to develop a length–weight relationship), then released.

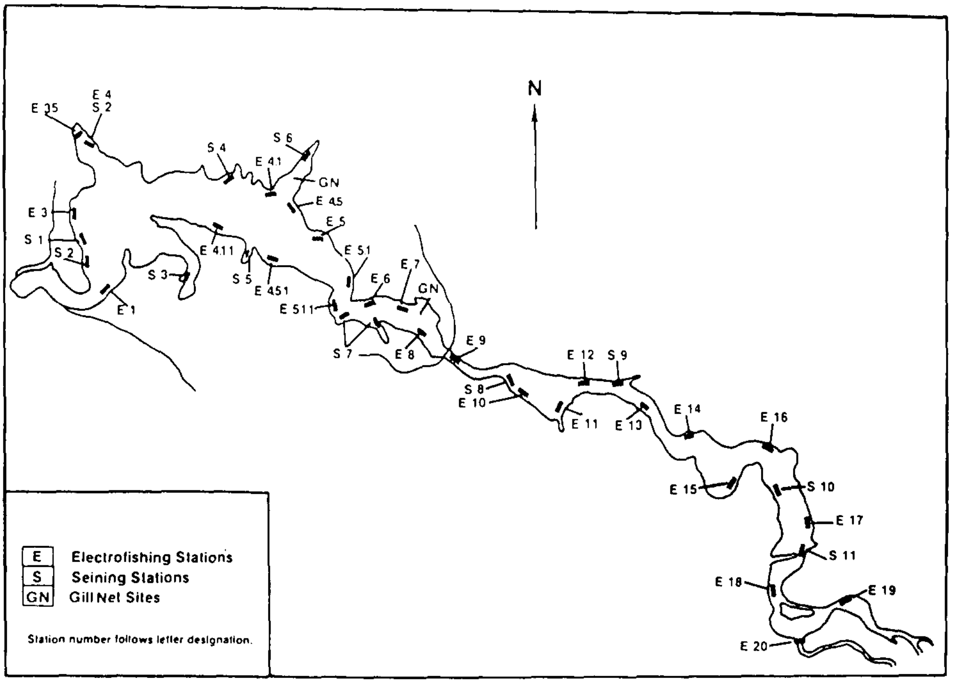

Fig. 1. Electrofishing, seining and gillnetting stations on Britton Reservoir.

Seining

Shoreline seining was conducted to supplement the electrofishing surveys, particularly for young-of-year (YOY) fishes. The seining was concentrated at 11 stations (Fig. 1) using a 1.2 × 9.1 m (4 × 30 ft) seine with 6.4-mm Ace mesh from June through October 1984, on a weekly basis. Three seine hauls were made at each station and the first 50 YOY fish and all larger fish of each species were measured; the remainder were counted, then released.

Gillnetting

We gillnetted in Britton Reservoir on a monthly basis from March 1983 through December 1984, except for May 1983. We stratified our sampling into three broadly defined periods. Gillnetting that occurred between sunrise and sunset was defined as a daytime set. Sampling periods encompassing sunrise or sunset were defined as dawn or dusk sets, respectively. During all sampling periods, nets were fished for a minimum of 4 h. We set gillnets in two locations: Cayton Cove and near the Highway 89 boat ramp (Figs. 1 and 2). All sets were made in Cayton Cove between June and September because heavy recreational use in the reservoir precluded sampling near the boat ramp. Vertical water-

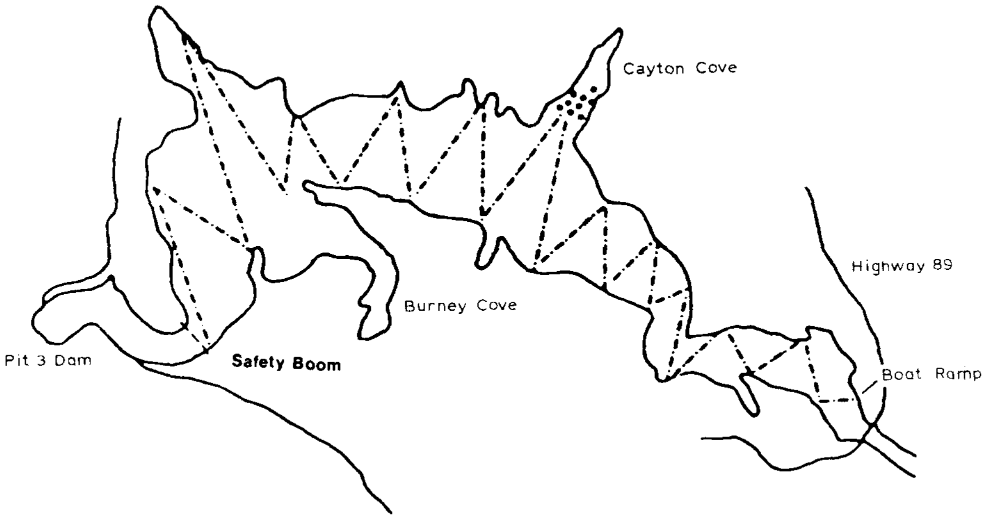

Fig. 2. The track of the Britton Reservoir mobile hydroacoustic surveys (dashed line) and location of fixed aspect transducers (o) in Cayton Cove. The asterisk (*) indicates the location of the single transducer used in the June 1983 fixed aspect survey.

temperature profiles were taken during each gillnet survey except during May and June 1983.

We conducted daytime sets in all months, except August and September 1983, when only dawn and dusk sets were made. All three time periods were sampled during the months of June and October 1983 and February and June 1984 in conjunction with hydroacoustic surveys. We also sampled all three time periods in July 1983.

We used surface (3–5 nets), mid-water (1–2 nets) and bottom (1–2 nets) experimental mesh gillnets. On most occasions we used 5, 2 and 2 nets, respectively. The top lines of the mid-water nets were set 4 m below the surface. Bottom nets were set in 8–16 m of water. Sampling prior to June 1983 did not include mid-water nets. Surface and mid-water nets were 36.6-m long by 1.5-m deep and were composed of equal length panels of 20, 25, 32, 44, 50, 60, 64, 76, 83, 102, 121 and 152 mm stretch-mesh monofilament nylon netting. Bottom nets were 38-m long by 1.8-m deep and were composed of equal length panels of 38, 50, 64, 76 and 102 mm stretch mesh.

As nets were lifted, fish were removed, measured (standard length $\pm$ 1 mm), and the mesh size noted. For the surface nets only, the depth of capture and the distance from the top of the net to the fish were also noted. Biomass estimates are only presented for the surface nets because in open water bald eagles are only capable of capturing fish near the surface (Todd et al., 1982). We calculated size selectivities of surface, mid-water and bottom gillnets for the 6 species most often captured, using methods described in Gulland (1969).

Hydroacoustics

We used two hydroacoustic techniques. The first was a downward-facing mobile mode in which a transducer was mounted in a hydrodynamically designed V-fin suspended 1 m below the water surface and towed at approximately 3 knots. The second was an upward-facing, stationary mode in which a transducer was mounted on a float and anchored 1 m from the bottom. The mobile hydroacoustic surveys permitted sampling over a much wider area than gillnetting; the stationary mode permitted continuous sampling at one location to examine diel distribution, particularly near the water surface. The downward-facing, mobile mode and the upward-facing, stationary mode are not directly comparable, but provide complementary data. The mobile downward mode did not sample the upper 2 m of the water column; the stationary upward mode did not sample the lower 2 m of the water column. Gillnets were set immediately after the hydroacoustic surveys were conducted. Gillnets provided information on species composition and relative abundance.

Mobile surveys were conducted on Britton Reservoir on 28 and 29 June 1983; 11, 12 and 14 October 1983; 11 and 12 February 1984. A dual-beam transducer with beam widths of 6° and 15° was used during the 1983 mobile surveys. The signal was transmitted on the 6° transducer and received on the 15° transducer. In the February 1984 mobile survey, however, the 15° transducer failed, so the survey was conducted using the 6° transducer to transmit and receive the signal. The return signals were displayed on a chart recorder and an oscilloscope and processed by a digital echo integrator (BioSonics Inc., Model 120; see Burczynski (1979) and Burczynski et al. (1987) for details concerning the mobile hydroacoustic techniques). During each survey we collected data at dawn, dusk and during the afternoon (day survey). Each survey was approximately 3 h in length and consisted of two transects; however, only one downstream transect was conducted in October during the day, owing to the limited number of daylight hours. The first transect began at the boat ramp area immediately below the Highway 89 bridge and proceeded downstream to the boom (Fig. 2) at approximately 1.65 m s^{-1} (3.25 knots). The second transect followed the same track as the first from the boom to the boat ramp. For the dawn survey, the first transect was timed to arrive at the boom at sunrise (pre-dawn survey) where the return track began (post-dawn). The dusk survey was conducted to arrive at the boom at sunset (pre-dusk) where the return track began (post-dusk).

In June 1983, one transducer was used to evaluate the upward-facing stationary mode for use in Britton Reservoir. This preliminary study showed the method to be successful in defining targets in the upper 2 m of the water column. After this initial success, eight transducers in the stationary mode were deployed in Britton Reservoir at Cayton Cove (Fig. 2) on 12 and 13 October 1983, 12 and 13 February 1984, and 6 and 7 June 1984. Each 15° transducer was deployed with a float collar and anchor, approximately 1 m above the bottom at depths ranging from 7 to 13 m (mean, 9.9) depending on location and water surface elevation. The fixed-aspect sampling array was split into four pairs of transducers and connected to two chart recorders through a multiplexer (BioSonics, Inc., Model 151). The multiplexer activated each pair of transducers sequentially on a continuous cycle. Sampling was concentrated at dawn, day and dusk in October and February, but ran continuously for 24 h in June 1984. During the initial evaluation procedure in June 1983, sampling was conducted continuously from 1400 to 2318.

The depth of each target, for the stationary mode surveys, was measured relative to the surface, directly on the chart recordings. Targets were summed for each hour. Target density was calculated as the number of targets m^{-3} h^{-1} over four depth intervals (m): 0–0.5, 0.5–2.0, 2.0–5.0 and 5.0–10.0. Target densities for depth > 10 m are not presented because the mean depth of the transducers was approximately 10 m and only 3 targets were observed below 10 m.

RESULTS

The fish fauna of Britton Reservoir was dominated by four native fishes (78% by number); however, three introduced fishes were also important (18%). In all, we collected 21 species in the course of the study by electrofishing. Seven species comprised approximately 96% of the catch by number and 84% by biomass (Table 1). Hardhead, Sacramento squawfish, Sacramento sucker and tule perch were found at least once at each of the 27 stations. Black crappie, largemouth bass and bluegill were found at 25, 24 and 22 of the stations, respectively, at least once during the study. However, the distribution of these species was not uniform (Table 2). The native species hardhead, Sacramento sucker and tule perch were significantly more abundant (χ^2 test, $P < 0.001$) in the upper, more riverine portion of the reservoir. One-third of the Sacramento sucker were collected at Station 20, which was not in the reservoir proper but in the mouth of Hat Creek. Of the remaining sucker, slightly more than half were captured in the upper reservoir. One half of the tule perch were captured in Stations 19, 20, 21, 22. Sacramento squawfish were slightly more abundant upstream (but not significantly, $P = 0.227$). Largemouth bass, black crappie, and bluegill were most abundant (χ^2 test, $P < 0.001$) in the lower, more lacustrine portion of the reservoir.

Catch per unit effort (CPUE) for numbers and biomass in the electrofishing samples for the seven most abundant species, as well as all species combined, generally peaked between June and September (Fig. 3). The increase in CPUE for numbers in the summer and early fall was owing to the appearance of YOY; however, biomass and numbers were correlated, which indicates the presence of both YOY and adult fish. Three exceptions to this trend were noted: (1)

TABLE 1

The seven most abundant species by number and percent collected in Britton Reservoir by electrofishing and seining. The associated biomass (g) is presented for electrofishing

Species	Electrofishing				Seining	
	No.	%	Biomass	%	No.	%
Tule perch (*Hysterocarpus traski*)[N]	2130	37.1	25705	3.0	2794	12.7
Hardhead (*Mylopharodon conocephalus*)[N]	1120	19.5	80921	9.4	8406	38.3
Sacramento sucker (*Catostomus occidentalis*)[N]	605	10.6	452884	52.9	4990	22.7
Sacramento squawfish (*Ptychocheilus grandis*)[N]	588	10.3	68796	8.0	2503	11.4
Black crappie (*Pomoxis nigromaculatus*)[I]	457	8.0	24398	2.9	519	2.4
Bluegill (*Lepomis macrochirus*)[I]	322	5.6	3614	0.4	886	4.0
Largemouth bass (*Micropterus salmoides*)[I]	269	4.7	66561	7.8	1226	5.6
Total of all species collected	5337		856831		21975	

[N], native species; [I], introduced species.
Other species collected were: green sunfish, *Lepomis cyanellus* (Rafinesque)[I]; golden shiner, *Notemigonus crysoleucus* (Mitchill)[I]; rainbow trout, *Salmo gairdneri* (Richardson)[N], carp, *Cyprinus carpio*[I]; white crappie, *Pomoxis annularis* (Rafinesque)[I]; *Pit Klamath brook lamprey, *Lampetra lethophaga* Hubbs[N]; rough sculpin, *Cottus asperimmus* (Rutter)[N]; marbled sculpin, *C. klamathensis* (Gilbert)[N]; California roach, *Lavinia symmetricus* (Baird and Girard)[N]; Pit sculpin, *C. Pitensis* (Bailey and Bond)[N]; *channel catfish, *Ictalurus punctatus* (Rafinesque)[I]; brown trout, *S. trutta* (Linnaeus)[I]; *tui chub, *Gila bicolor*[N]; speckled dace, *Rhinichthys osculus* (Girard)[N]. Two additional species were collected while seining: brown bullhead, *Ictalurus nebulosus* (Lesueur)[I], and black bullhead, *I. melas* (Rafinesque)[I].
*Not collected in seine hauls.

28% of all tule perch collected were captured in the March 1983 sample; (2) the biomass CPUE for squawfish exhibited two peaks: one in February and the second in October; (3) largemouth bass exhibited three biomass peaks: one in April (during spawning); one in June and July; and a final peak in September and October.

The patterns of species distribution and abundance in the seine catches were similar to those observed for the electrofishing samples; however, the seine catch was dominated by YOY fishes. Twenty species of fish were collected by seining. The seven most abundant fishes were of the same species as collected by electrofishing; however, the rank order was different (Table 1). Although all species were found throughout the reservoir, YOY and juvenile hardhead and Sacramento sucker were most abundant in the seine hauls in the upper portion of the reservoir whereas the remaining species were all more abundant in the lower portion of the reservoir.

We captured a total of 14 species in the gillnets during the study. Surface nets captured 11 species, mid-water nets 8 species, and bottom nets 9 species (Table 3). Surface net catches were numerically dominated by hardhead. However, hardhead and Sacramento sucker comprised 72.3% of the biomass. Both mid-water and bottom-net catches were dominated by tule perch.

TABLE 2

Numbers of the seven most abundant fishes collected in Britton Reservoir by electrofishing at each station. A χ^2 test was used to compare upper and lower reservoir numbers for each species

Station	TP[a]	HH	SKR	SQ	BC	BG	LMB
Lower reservoir							
1	75	25	15	35	14	17	36
2	52	5	10	27	6	7	6
3	23	10	9	26	5	6	11
4	7	3	17	6	6	1	1
5	18	5	13	24	7	13	4
6	64	18	14	10	33	9	8
7	142	6	25	18	119	15	58
8	34	7	6	16	58	34	32
9	32	9	17	54	13	15	29
10	19	10	6	29	4	49	10
11	19	5	11	22	6	11	8
12	42	4	9	19	4	16	9
13	5	17	5	8	9	37	2
14	29	13	29	14	38	9	1
15	13	12	6	2	37	31	5
Total	574	149	192	310	395	270	220
16	173	82	24	25	3	30	4
17	82	31	20	10	7	2	2
18	62	104	34	39	6	13	3
19	253	64	30	45	4		5
20	273	80	28	30	34	1	1
21	216	94	9	18	7	4	6
22	286	32	21	35	20	1	21
23	82	46	10	18	7		4
24	75	48	14	14	4	1	
25	47	96	8	19	6		3
26	6	275	12	19			
27	1	19	203	6			
Total	1556	971	413	278	98	52	49
χ^2	705.1	709.0	138.8	1.99	97.7	104.2	75.8
P	<0.001	<0.001	<0.001	0.227	<0.001	<0.001	<0.001

[a]TP, tule perch; HH, hardhead; SKR, Sacramento sucker; SQ, Sacramento squawfish; BC, black crappie; BG, bluegill; LMB, largemouth bass.

Nearly all species collected in the surface gillnets were represented by individuals that were entangled less than 50 cm from the surface (Table 4). This is the maximum distance eagles are likely to forage in deep water (G. Hunt, personal communication, 1983).

The species composition of gillnet catches varied with time of day (Table 3). Six species were captured in the surface gillnets during day sets, but the

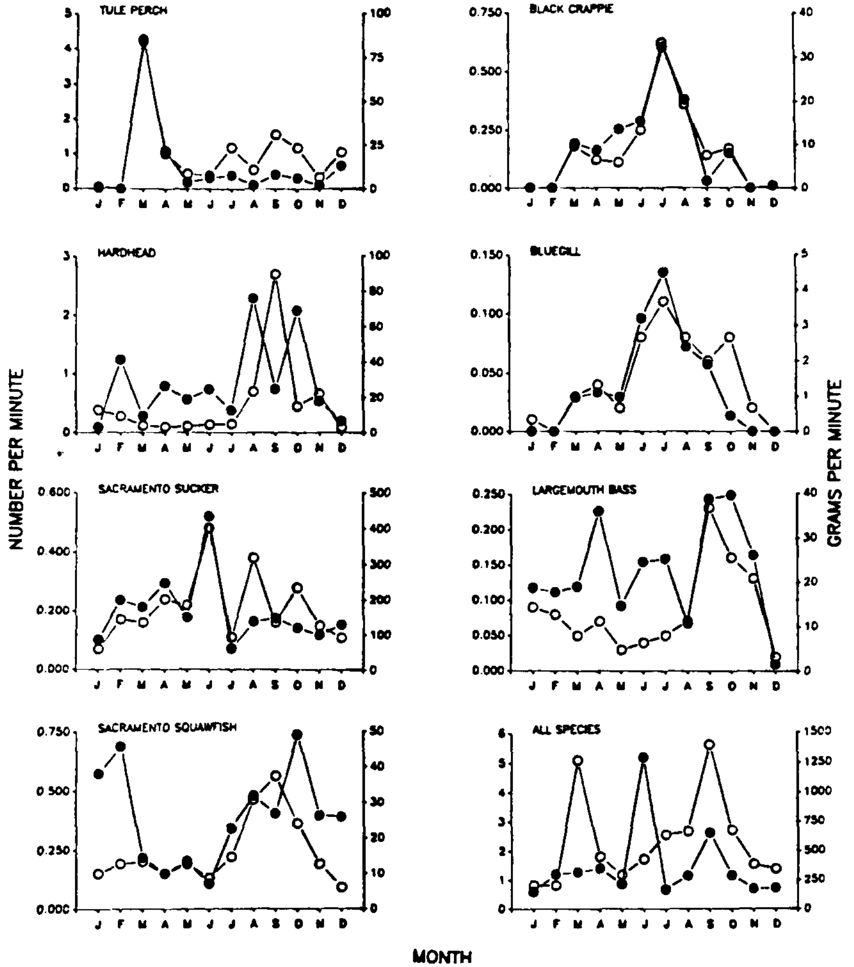

Fig. 3. Catch per unit effort for numbers (open circles) and biomass (closed circles) for the 7 most abundant species and all species combined collected by electrofishing in Britton Reservoir. Note Y-axis scale differences.

species composition was strongly dominated by hardhead (64% by number) and sucker (23% by number). During dawn sets, the surface gillnet catches captured 8 species, but the catch consisted primarily of hardhead (41% by number) and tule perch (29% by number). Dusk sets captured 10 species and were dominated by hardhead (39%), with tui chub (21%) and black crappie (12%) also present in numbers.

While hardhead dominated the catch in surface gillnets, tule perch dominated the catch in mid-water and bottom gillnets. Both day and dusk sets of mid-water nets were numerically dominated by tule perch (49 and 53%, respectively), though day sets captured more species (7 vs. 3). Black crappie

TABLE 3

Species composition for dawn, day and dusk sets of surface, mid-water and bottom gillnets

	Surface		Mid-water		Bottom	
	N	%	*N*	%	*N*	%
Dawn						
Hardhead	24	41	5	14	11	4
Sacramento squawfish	4	7	3	8	24	8
Tule perch	17	29	10	28	253	82
Tui chub	5	9			8	3
Sacramento sucker	3	5	1	3	8	3
Black crappie	3	5	9	25	2	1
White crappie			7	19		
Rainbow trout	1	2				
Bluegill			1	3	1	1
Carp					1	1
Largemouth bass	1	2				
Total	58		36		308	
Day						
Hardhead	47	64	26	18	54	11
Sacramento squawfish	6	8	8	6	33	7
Tule perch	1	1	70	49	369	74
Tui chub			1	1	21	4
Sacramento sucker	17	23	7	5	10	2
Black crappie			19	13	10	2
White crappie			12	8	1	1
Rainbow trout	1	1				
Brook charr	1	1				
Total	73		143		498	
Dusk						
Hardhead	54	39	1	6		
Sacramento squawfish	9	6			2	3
Tule perch	9	6	9	53	64	86
Tui chub	29	21			4	5
Sacramento sucker	13	9			2	3
Black crappie	17	12	7	41		
White crappie	2	1				
Rainbow trout	3	2				
Golden shiner	3	2				
Bluegill					2	3
Brown trout	1	1				
Total	140		17		74	

TABLE 4

Depth distribution (cm below surface) of fishes collected in surface gillnets in Britton Reservoir, March 1983–December 1984. Mean depth ($\bar{D}$), standard deviation (SD) and percentage of the catch are presented for each species

Mid point Depth (cm)	Species												
	HH[a]	SQ	TC	TP	SKR	BC	WC	LMB	RT	BT	EB	GS	Total
5	2			1									3
10	5	2				2							10
20	7	2	2	1								1	13
30	10	4	3	1	1	2	1						22
40	17	2	2	2		2			5				30
50	6	1	3	1	1	1				1			14
60	13	1	2		1	2			1			1	21
70	8	2	4	3	3	1						1	22
80	16	2	2	4	3	5							32
90	4	1	3	1	1	1		1					12
100	6		2		3	2							13
110	9	1	1	6									17
120	3	3	3	2	3						1		15
130	4		4	2	1								11
140	9		5	2	7	1							24
150	4				4		1						9
Total	123	21	36	27	28	19	2	1	6	1	1	3	268
D	71	59	86	83	109	65	90	90	43	47	120	50	
SD	40	37	40	40	36	33	-	-	8	-	-	26	
%	45.9	7.8	13.4	10.1	10.4	7.1	0.7	0.4	2.2	0.4	0.4	1.1	

[a]HH, hardhead; SQ, Sacramento squawfish; TC, tui chub; TP, tule perch; SKR, Sacramento sucker; BC, black crappie; WC, white crappie; LMB, largemouth bass; RT, rainbow trout; BT, brown trout; EB, brook charr; GS, golden shiner.

(41%) were the second most abundant species in dusk sets. Hardhead (18%) and black crappie (13%) were next in numerical abundance in day sets. Dawn sets of mid-water nets were not strongly dominated by a single species. Tule perch (28%), black crappie (25%), white crappie (19%) and hardhead (14%) made up the bulk of dawn catches. Bottom net catches were numerically dominated by tule perch for dawn (82%), day (74%) and dusk (86%) sets.

Species richness of gillnet catches varied from season to season. The number of species in surface gillnets was generally greatest in summer and fall. Few fish were captured in the winter and spring. Hardhead were captured in surface gillnets in all but 3 months in which fish were caught (March, April and May 1984). Mid-water catches rarely included more than 3 species. The most diverse catches in the mid-water nets occurred in October 1983 and February 1984 when 6 species were captured. Species composition of bottom gillnet catches were similar to those of mid-water gillnet catches. The most diverse catches in the bottom nets generally occurred in the summer and fall.

CPUE, calculated as number of fish captured h^{-1} and g of fish captured h^{-1}

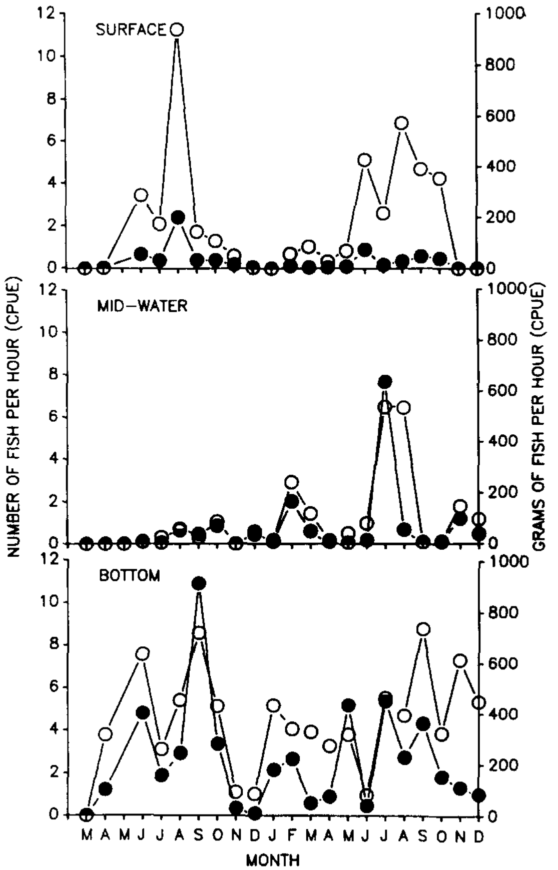

Fig. 4. Catch per unit effort for number (open circles) and biomass (closed circles) for all species combined as fish per hour for surface, mid-water, and bottom gillnet catches on Britton Reservoir.

(Fig. 4), varied during the study. Surface CPUE peaked during June–October in both years. Mid-water net CPUE was highly variable but appeared to peak in October. Minor peaks occurred in November or December and in February. Bottom-net catches were highly variable. Peak catches occurred in July–September. The general trend appeared to be for high catches in the summer and fall, especially for surface nets. This pattern presumably reflected an increase in surface activity of fishes during the summer and fall that contributed to their availability to bald eagles.

CPUE varied on a diel basis for surface, mid-water and bottom gillnets (Fig. 5). Surface net catches were highest at dusk, lowest during the day, and intermediate at dawn. Mid-water net catches showed the opposite trend and decreased from day to dawn to dusk. Bottom-net catches were highest at dawn, intermediate during the day, and lowest at dusk. These trends indicate a diel cycle in fish behavior. Most species were presumably inactive and/or on the

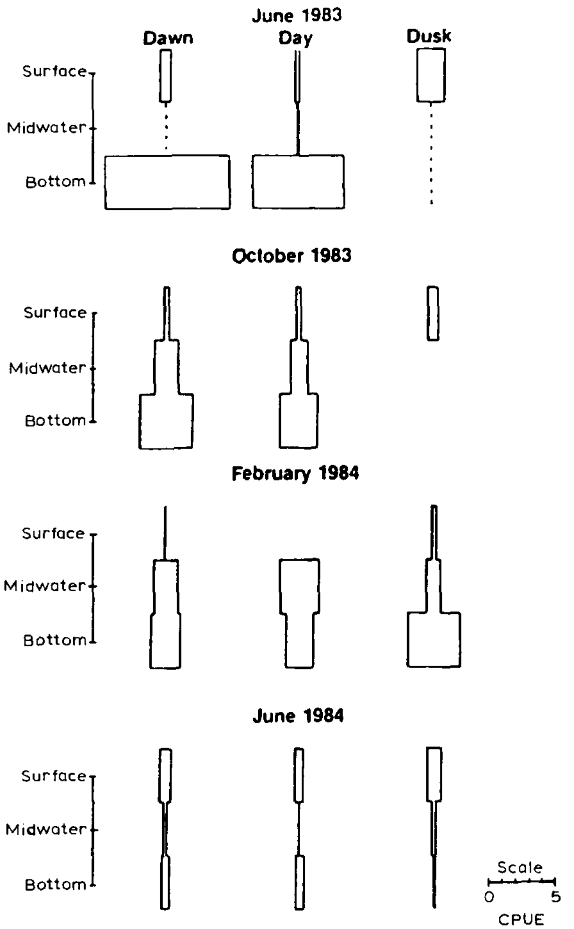

Fig. 5. Catch per unit effort for surface (S), mid-water (M) and bottom (B) gillnets during dawn, day and dusk sets immediately after the fixed aspect hydroacoustic surveys.

bottom during the day, migrated to the surface at dusk, and returned to the bottom some time after daylight.

Our size-selectivity analysis indicated that YOY fishes were probably too small for all of the nets and that the bottom nets were somewhat biased against capture of the largest tui chub, Sacramento squawfish, Sacramento sucker and hardhead. For most species, individuals older than 1 year were susceptible to capture by the gillnets we used.

The mobile hydroacoustic surveys demonstrated a marked seasonal trend in vertical fish distribution with a less pronounced diel distribution (Fig. 6). In June 1983, fishes were most abundant between 2 and 5 m. In October 1983, fishes were most abundant between 10 and 20 m. The highest density of fishes in February, was between 2 and 5 m, but the fishes were more uniformly dis-

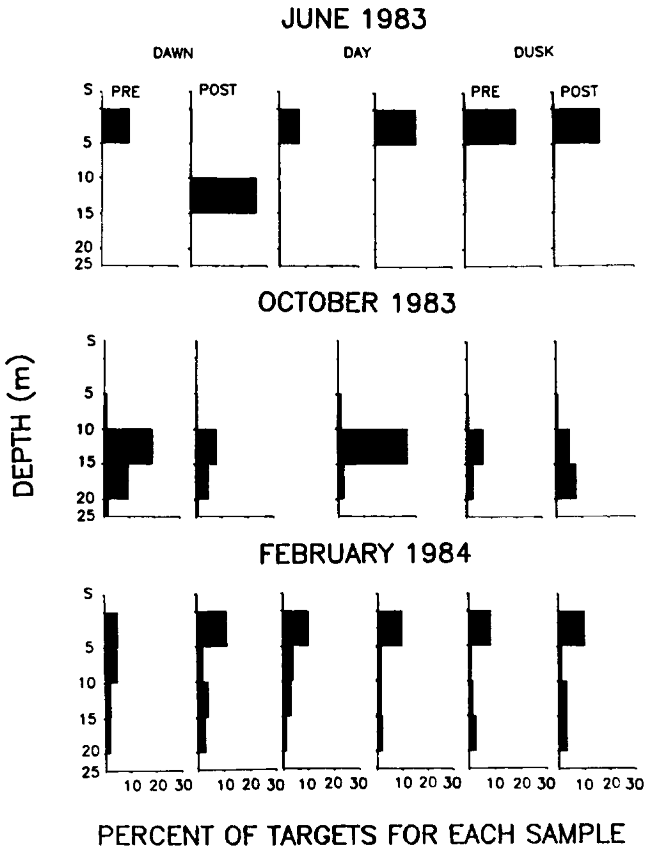

Fig. 6. Relative density of targets at each depth interval and time of day for the 3 mobile hydroacoustic surveys conducted in Britton Reservoir.

tributed than in either June or October. On a diel basis the relative densities at each depth interval remained much the same, but there were two exceptions. In June 1983 there was a shift in abundance from 2 to 5 m in the pre-dawn survey to 10–15 m just after sunrise. In October 1983 fishes concentrated between 10 and 15 m during the day, whereas the fishes were found between 10 and 20 m in the dawn and dusk surveys.

During the mobile surveys, mean fish densities were 3.6 fish 1000 m^{-3} in June 1983 and 37.4 fish 1000 m^{-3} in October 1983. February 1984 densities cannot be compared with June or October because of the failure of the 15° beam width transducer and the automatic bottom-tracking function that caused a higher intensity signal to be generated.

There was a marked seasonal change in vertical distribution in the stationary mode surveys. During our surveys in late June 1983 and early June 1984, fishes were found throughout the water column, with many fishes in the upper 2 m and some fishes always present in the near-surface zone (<0.5 m). In October 1983 and February 1984, fishes were found deeper in the water column,

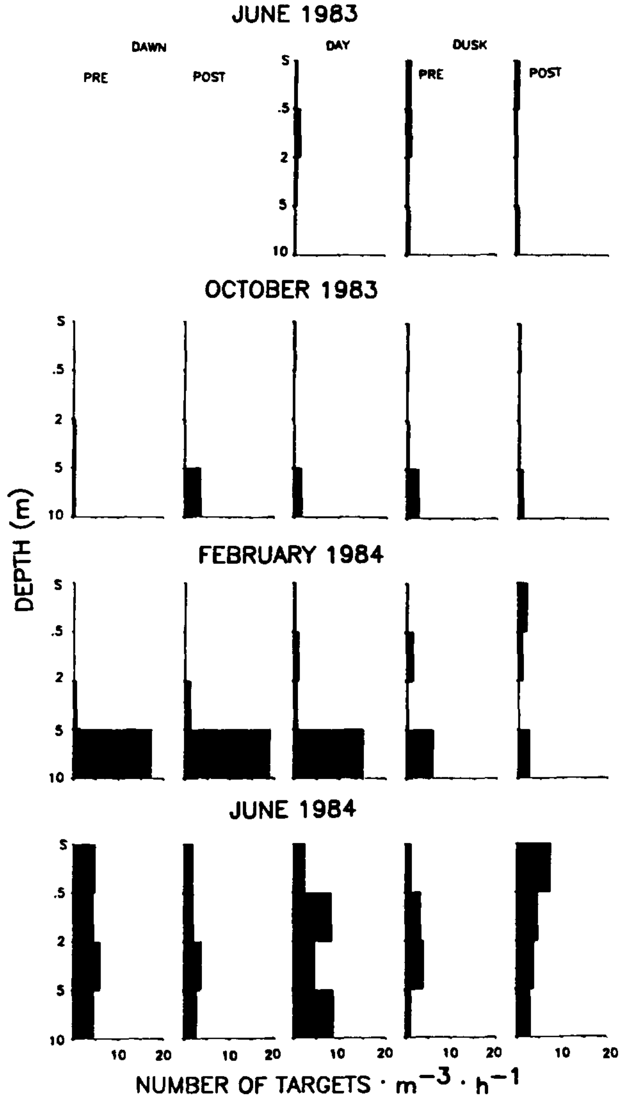

Fig. 7. Relative frequency of targets for each depth interval and time of day for the 4 fixed aspect hydroacoustic surveys conducted in Britton Reservoir in Cayton Cove.

generally below 5 m, with a small proportion in the upper 2 m (Fig. 7). Overall, during the stationary mode surveys there was a marked seasonal difference in the number of targets detected that reflected changes in both activity and relative abundance. The highest number of targets was detected in late June 1983, followed in decreasing order by early June 1984, October 1983 and February 1984. On a diel basis the highest number of targets was observed at dusk, the lowest during the day and an intermediate number at dawn.

The trends in the hydroacoustic surveys generally agree with gillnet surveys. The stationary mode surveys covered the same area of the water column as the surface and mid-water gillnets. Using both methods, surface activity was highest in the summer and lowest in the fall and winter. Because gillnetting was conducted immediately following the hydroacoustics, the species composition of the targets is probably the same as presented in Table 2. Mid-water activity was highest in October 1983 and February 1984. The mobile surveys cover the zone immediately below the surface nets and mid-water area. There is general agreement between the mobile surveys and gillnets for June 1983 and October 1985, but not for the February 1984 sample.

We compared eagle diets, determined from prey remains in and below nests, below primary perches, and from time-lapse photography (Hunt et al., (1988) with the species abundance of the electrofishing and gillnetting surveys (Table 5). The relative abundance of fish in the gillnets was significantly correlated with the eagle diet ($P = 0.039$), while the electrofishing abundance was not correlated with diet ($P = 0.574$).

Surface-water temperature was lowest in January 1984 (5.5°C) and highest in July 1984 (24.0°C). Temperatures were isothermal throughout the water column in November and December 1983 and January, February, March and April 1984. The maximum temperature differential between the surface and the bottom occurred in July 1984 when surface temperatures reached 24.0°C and temperatures were 15°C near the bottom. Although there is a thermal

TABLE 5

Rank of fishes in bald eagle prey remains (Hunt et al., 1988) and fishes collected by electrofishing and gillnets which were larger than the minimum size in bald eagle prey remains[a]

Species	Diet	Electrofishing	Gillnet
Sacramento sucker	1	1	3
Hardhead	2	3	1
Ictalurids sp.	3	10	10
Tui chub	4	11	2
Squawfish	5	6	6
Crappie sp.	6	5	4
Tule perch	7	2	5
Trout sp.	8	8	7
Carp	9	9	10
Largemouth bass	10	4	9
Centrarchids sp.	11	7	8
Correlation (r)		0.191	0.626
Probability (P)		0.574	0.039

[a]Minimum standard length of fishes in eagle prey remains: Sacramento sucker ≥ 200 mm, hardhead ≥ 250 mm, black crappie ≥ 130 mm, Sacramento squawfish ≥ 300 mm, tule perch ≥ 100 mm, largemouth bass ≥ 120 mm, bluegill ≥ 130 mm.

structure in Britton Reservoir, a classical thermocline did not form, probably owing to the low retention time of the reservoir.

DISCUSSION

While 24 species of fish were collected in the reservoir, 9 species made up more than 96% of the catch by all methods. The four most abundant species (tule perch, Sacramento sucker, Sacramento squawfish and hardhead) were all natives and comprised over 75% of the catch. The other numerically important species were the native tui chub and introduced largemouth bass, bluegill, black crappie and white crappie. Because three different sampling methods were used, each with different biases, our sampling should be an accurate characterization of the fish assemblage present, although small, bottom fishes (particularly sculpins, *Cottus* spp) were undoubtedly not adequately sampled. In particular, it is likely that the introduced fishes were adequately sampled, as most of the species are characteristic of inshore areas (Moyle, 1976) so they should have been especially vulnerable to the electrofishing and seining. One introduced species, not collected during our survey, but now apparently common in Britton Reservoir is the smallmouth bass, *Micropterus dolomieui* (Lacepède). This bass was introduced illegally as our study was being completed (D. Weidlein, personal communication, 1985).

The native fishes have maintained their numerical dominance in the reservoir, despite repeated introductions of non-native species (files, CDFG, Region 1) and the establishment of reproducing populations of at least six introduced species. Introduced species can also move into the reservoir from upstream sources. Channel catfish, largemouth bass, green sunfish, bluegill and brown bullhead are all abundant in the Pit River upstream of the reservoir (Moyle and Daniels, 1982; Cooper, 1983; Herbold and Moyle, 1987).

Habitat use

The nine most abundant species in our samples can be found throughout Britton Reservoir and the species commonly occur together. Nevertheless, there were some differences in habitat use among the fishes that indicated at least some ecological segregation. Squawfish, hardhead, tule perch and sucker were found throughout the reservoir, but were most abundant in the more riverine upper half of the reservoir. These four native species coevolved in the Sacramento–San Joaquin river system which includes the Pit River (Moyle, 1976). The most abundant introduced species, largemouth bass, bluegill and black crappie were found primarily in the broader lower half of the reservoir where conditions were more lacustrine and similar to the habitats in which they evolved. Largemouth bass and bluegill were typically captured close to shore in shallow water near cover (typically fallen trees). Black crappie were also most abundant close to shore, but also were captured in off-shore gillnets. Tui chubs and white crappie were collected almost entirely in offshore gillnets. Although black and white crappie were collected in the surface gillnets, they were relatively more abundant in the mid-water and bottom nets. Squawfish, hardhead, sucker and tule perch were captured in both inshore and offshore samples, but their young of year were found mainly close to shore. The low vulnerability of small fishes to the gillnets (despite small mesh sizes) may have exaggerated this pattern. Sacramento sucker were by far the most abundant species collected in the lower portion of Hat Creek (Station 19) which is clear and relatively shallow.

Of the fishes caught in the gillnets, tule perch were most consistently found close to the bottom, while hardhead and sucker were most abundant near the surface. The abundance of sucker near the surface was surprising because sucker are generally considered to be a bottom-oriented species (Moyle, 1976). There was a general tendency for fishes to be more abundant in surface waters during the summer and in deeper waters during the winter. Peak abundances of most species, in all habitats, occurred in late summer and fall, presumably because the young of year had grown to sizes more vulnerable to capture. Biomass, however, was correlated with numbers for most species (Fig. 3) which indicates that in general, most size classes were proportionally represented.

How have native fishes maintained their dominance?

The main factor keeping the native fishes abundant and introduced fishes uncommon is the way in which the reservoir is operated for hydroelectric generation. Britton Reservoir is used to meet power production requirements during high demand periods. During the winter, when inflows are high and power demands low, the reservoir maintains a fairly constant level because water generally spills over the dam. From May through November, it is operated to meet daily and weekly peaks in demand for electricity. This means the water surface level can fluctuate up to 2 m on a weekly basis. This mode of operation makes it difficult for largemouth bass, crappie and bluegill to spawn successfully. These species all spawn in nest depressions in shallow water where the eggs and fry are guarded for 7–14 days. The water level fluctuations can cause the breeding adults to abandon nests that become either too deep or too shallow, can dewater nests completely, or drive young fish from cover, making them more vulnerable to predation (Aggus and Elliot, 1975; Romero and Allen, 1975; Mitchell, 1982). Dewatering may be particularly important, as between 1970 and 1984 known spawning areas of centrarchids were dewatered during the spawning season in at least 6 of the 14 years (Pacific Gas and Electric Co., 1985). These same factors may account for comparatively small numbers of tui chubs in the reservoir. Tui chubs spawn in inshore areas in early summer on aquatic plants (Kimsey, 1954; Kucera, 1978). In contrast, squawfish, hardhead and sucker all migrate into tributary streams to spawn in gravelly riffles.

These species have no parental care. The young fish often use the streams as nursery areas (Moyle, 1976), thus avoiding the loss of cover from predators that can occur in the reservoir as a result of water-level fluctuations. Tule perch also avoid the problem of fluctuating water levels because they are live bearers, producing large young that are relatively invulnerable to predation (Baltz and Moyle, 1982).

A well-developed thermocline does not form in Britton Reservoir owing to the low water-retention time resulting from the hydroelectric generation. The thermal structure is midway between a coldwater reservoir, that could favor a salmonid community, and a warmwater reservoir that would benefit the introduced centrarchid fishes. Thermal preferences of the centrarchids range from 26.6°C for largemouth bass to 31.0°C for bluegill (Houston, 1982). The native nongame fishes are also not favored by the thermal regime. Thermal preferences range from 26.0°C for Sacramento squawfish to 27.9°C for hardhead (Knight, 1985). However, the native fishes probably continue to dominate because the centrarchids are influenced by both the water-level fluctuations and a sub-optimal temperature regime.

What characteristics make native fishes available to eagles?

Bald eagles fed primarily on Sacramento sucker, hardhead and Sacramento squawfish, taking other large fishes only occasionally (Hunt et al., 1989). The abundance and size of these prey species were no doubt major contributing factors to their being taken by eagles. Thus, species composition of the gillnet catch was positively correlated with the species composition of Britton Reservoir eagle diets (Hunt et al., 1989). Equally important, however, was the availability of these fishes. During the summer and fall, the eagles can capture the above 3 species because they are common near the surface in open or shallow water. Hardhead were observed, slowly swimming or holding, in warm surface waters during gillnet surveys and were often observed at the surface of large pools in the river below Britton Reservoir (Hunt et al., 1989). In late spring and early summer these fishes become vulnerable to eagles when they spawn in shallow riffles of the tributary streams. In addition, the eagles apparently consume many fish that die following spawning. Hunt et al. (1989) found that post-spawning Sacramento sucker represented 52% of 132 carrion fishes during June–July surveys. Sacramento sucker, Sacramento squawfish, and hardhead are all captured on occasion by anglers who frequently kill them before discarding them (Hunt et al., 1989). The carcasses may then be consumed by the eagles, as noted in Maine by Todd et al. (1982). Elsewhere suckers of various species are important in the diet of bald eagles (Dunston and Harper, 1975; Todd et al., 1982; Haywood and Ohmart, 1986), presumably because their morphological and behavioral adaptations related to benthic feeding limit their ability to perceive attack from above (Swenson, 1979).

The introduced centrarchids probably do not contribute to the eagle diets, because while inshore these fishes seek shelter under overhanging vegetation or in fallen trees, which reduces their vulnerability to predation from above. Black crappie and white crappie were collected in open water; however, they were relatively more abundant in the midwater and bottom nets and were not subject to predation by the eagles. Only at dusk were black crappie active in the surface waters, but this corresponded to the reduced foraging activity of the eagles (Hunt et al., 1989).

On a diel basis, bald eagles appeared to forage most heavily in the early morning. Hunt et al. (1989) reported that the eagles delivered 43% of all prey items to the nest within 2 h of dawn and an additional 24% in the following 2-h period. This peak in foraging coincides with the relatively high surface activity of the fishes in the gillnets and fixed hydroacoustic surveys.

MANAGEMENT IMPLICATIONS

Management of the fish populations of Britton Reservoir has two main goals: (1) to maintain the large populations of nongame fishes in order to provide food for bald eagles; (2) to improve the sport fishery, especially for bass. Unfortunately, the two goals appear to be contradictory. If largemouth bass populations are greatly increased by either stabilizing the reservoir water levels during the spawning season or stocking juvenile bass, the increased predation on the juvenile native fishes is likely to decrease recruitment of hardhead and squawfish. This ultimately may mean less forage available for the breeding eagles and lowered reproductive success. Because the bald eagle is fully protected as an endangered species by both federal and state law, managing the reservoir fish populations for the benefit of eagles has priority over managing the reservoir to improve the fishery. Therefore, any attempt to increase the populations of introduced gamefishes would be ill-advised.

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