

Assessing Ecosystem Effects of Reservoir Operations Using Food Web–Energy Transfer and Water Quality Models

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ABSTRACT

We investigated the effects on the reservoir food web of a new temperature control device (TCD) on the dam at Shasta Lake, California. We followed a linked modeling approach that used a specialized reservoir water quality model to forecast operation-induced changes in phytoplankton production. A food web–energy transfer model was also applied to propagate predicted changes in phytoplankton up through the food web to the predators and sport fishes of interest. The food web–energy transfer model employed a 10% trophic transfer efficiency through a food web that was mapped using carbon and nitrogen stable isotope analysis. Stable isotope analysis provided an efficient and comprehensive means of estimating the structure of the reservoir's food web with minimal sampling and background data. We used an optimization procedure to estimate the diet proportions of all food web components simultaneously from their isotopic signatures.

Some consumers were estimated to be much more sensitive than others to perturbations to phytoplankton supply. The linked modeling approach demonstrated that interdisciplinary efforts enhance the value of information obtained from studies of managed ecosystems. The approach exploited the strengths of engineering and ecological modeling methods to address concerns that neither of the models could have addressed alone: (a) the water quality model could not have addressed quantitatively the possible impacts to fish, and (b) the food web model could not have examined how phytoplankton availability might change due to reservoir operations.

Key words: stable isotope analysis; CE-QUAL-W2; Shasta Lake; temperature control device; interdisciplinary modeling; food web modeling; energy transfer.

INTRODUCTION

Growing concern over the downstream physical and chemical effects of dams on regulated rivers and on the life history of resident and migratory fishes has prompted serious public debate about the efficacy of removing dams for ecosystem restoration

(Shuman 1995; Collier and others 1996; Larmer 1999). In some instances, public dependence on the commodities and services provided by dams and their reservoirs preclude dam removal in the short term, especially in the case of large reservoirs in the western United States (Collier and others 1996). Instead, managers have sought to learn how to lessen the riverine impacts of large dams by evaluating alternative operational regimes (Collier and others 1996; Stanford and others 1996; Poff and

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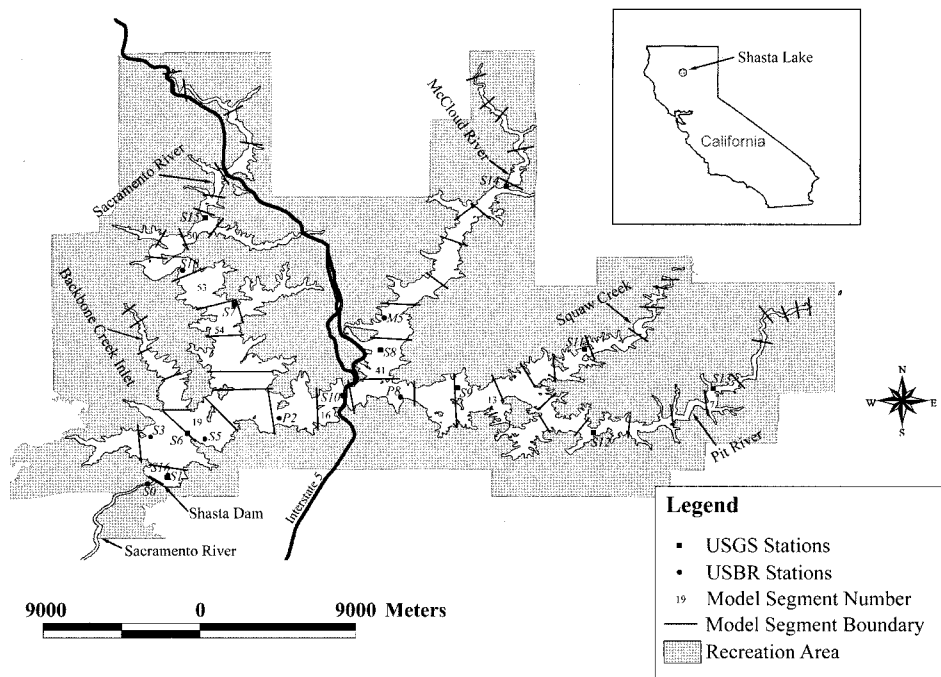


Figure 1. CE-QUAL-W2 representation of Shasta Lake. Note: Main body of lake includes area downstream of sampling stations S7 and S10.

others 1997). These ecosystem experiments not only have the potential to identify more sustainable dam management scenarios, but also offer the opportunity to learn how lotic and lentic ecosystems respond to large-scale perturbations. The tremendous influence that dams have on regulated rivers (Covich 1993; Naiman and others 1995; Power and others 1996; Stanford and others 1996) suggests that dam managers hold the power to conduct potent and enlightening manipulations of both downstream and upstream ecosystems. Such ecosystem experiments can be a powerful means of evaluating and predicting environmental change (Ward and Stanford 1984, 1987; Carpenter and others 1995).

Because of the socioeconomic compromises that are required when dam operations depart from their primary historic functions in water management and hydropower generation, new dam operations have usually been applied to ecosystems inhabited by endangered species (for example, Glen Canyon Dam on the Colorado River, Flaming Gorge Dam on the Green River, and Blue Mesa Dam on the Gunnison River). When dams are identified as jeopardizing species, managers are compelled to seek alternative operations. Unfortunately, the urgency of protecting rare species has made it difficult to (a) gather sufficient premanipulation data for science to fully benefit from these management experiments, and (b) obtain a sufficient understanding of the ecosystem for managers to forecast impacts before taking action.

In reality, the inadequacy of the existing knowledge base is a common, if not universal, problem in natural resources management (Lee 1993; Gunder-son and others 1995; Christensen and others 1996), prompting a new paradigm, "adaptive management" (Holling 1978; Walters 1986), in which management proceeds despite considerable uncertainty about the structural and functional characteristics of the ecosystem. Adaptive management uses deliberate management changes as experiments (Hilborn and others 1995) and involves research to evaluate these management actions; it then revises these actions to adapt to environmental and societal change, as well as new information provided by research (Stanford and Poole 1996). An essential step in this approach is to capture existing understanding about the system in the form of an explicit model or models. Predictions from the model(s) can then be compared to actual management outcomes, with divergence used as a basis for further learning. In this paper, we present a set of models for synthesizing existing knowledge and a framework for predicting physical, chemical, and biological responses of reservoir ecosystems to changes in water storage and release regimes.

New Dam Operations at Shasta Lake

Shasta Lake, the largest (11,940 ha) reservoir in California (Figure 1), was formed when a dam was constructed on the Sacramento River in 1945. The dam prevented chinook salmon (*Oncorhynchus*

tshawytscha) from migrating to their native spawning habitat upstream of the dam and thus contributed to their decline. In 1989, the winter-run chinook were listed as threatened under the Endangered Species Act (its status was changed to endangered in 1994), prompting managers to seek mitigation measures to ensure the continued existence of the salmon. Their approach was to alter dam operations, with the goal of enhancing survival of the salmon downstream of the dam. To improve downstream thermal conditions for the salmon the US Bureau of Reclamation (USBR) installed a temperature control device (TCD) on Shasta Dam in 1997 (Vermeyen 1998). This device gave the USBR greater flexibility in selecting withdrawal depths and hence release temperatures while maintaining hydropower generation. In changing withdrawal depths, the operation of this facility for downstream water temperature management had the potential to change in-reservoir thermal, water quality, and biological patterns. Managers were concerned that these changes could affect the sport fishery at Shasta Lake that includes rainbow trout (*Oncorhynchus mykiss*) and several basses (*Micropterus* spp.).

Although management concerns at Shasta Lake and elsewhere (Johnson and others 1999) have focused on a single or small number of species (that is, sport fishes), the potential effects of new dam operations include alteration of nutrient budgets, thermal regimes, and primary production, and these alterations may have indirect effects on the species of interest. Because dam operations have the potential to disrupt complex trophic linkages (Wootton and others 1996) via alteration of physicochemical processes, our analysis was an interdisciplinary one that merged the strengths of engineering and ecological perspectives by combining a process-oriented ecosystem model with a more structure-oriented food web model.

We hypothesized that changes in withdrawal depths could alter temperature and nutrient dynamics in the reservoir. Earlier modeling showed that direct thermal effects on fishes would be negligible because temperature changes were primarily deep in the hypolimnion, a region inhabited by few fish (Hanna and others 1999). However, changes in nutrients and phytoplankton production could still alter energy flow within the reservoir food web. Organisms dependent upon phytoplankton-based energy pathways could be expected to be most sensitive to the bottom-up effects of new dam operations, whereas other consumers more dependent on terrestrial-based carbon inputs could be relatively unaffected by the new operations.

METHODS

We used a linked modeling approach (Saito and others 1999) in which (a) a specialized reservoir water quality model (CE-QUAL-W2) (W2) (Cole and Buchak 1995) was used to forecast dam-induced changes in phytoplankton production, and (b) a food web–energy transfer model was used to propagate predicted changes in phytoplankton up through the food web to the predators and sport fishes of interest. The food web model employed a trophic transfer efficiency with the assumption that only 10% of available production at a particular trophic level was available at the next trophic level (Slobodkin 1968; DeAngelis 1992; Christensen and Pauly 1993; Pauly and Christensen 1995; Begon and others 1996):

$$\text{Trophic transfer efficiency} = \frac{P_n}{P_{n-1}} \approx 0.10 \quad (1)$$

where

P_n = total production available at trophic level n (joules [J])

P_{n-1} = total production available at trophic level $n - 1$ (J)

The trophic transfer efficiency was used to estimate the energy transferred from phytoplankton to other species in the food web. We were thus able to investigate the relative impacts of changes in W2-predicted phytoplankton production due to altered reservoir operations on in-reservoir sport fish and other species.

Reservoir Water Quality Model

W2 is a two-dimensional hydrodynamic and water quality model developed and distributed by the US Army Corps of Engineers (USACE). The model generates vertical profiles of modeled constituents for longitudinal segments throughout the reservoir. The W2 model was selected because of its strong hydrodynamic and thermal modeling capabilities, which were an important part of earlier modeling efforts (Hanna and others 1999). In addition, W2 allows the prediction of nutrients and phytoplankton production through time and space. Details of the development and calibration of the W2 model for Shasta Lake are given in Hanna and others (1999) and Bartholow and others (forthcoming).

The W2 model of Shasta Lake consisted of 63 segments with up to 51 vertical layers (Figure 1).

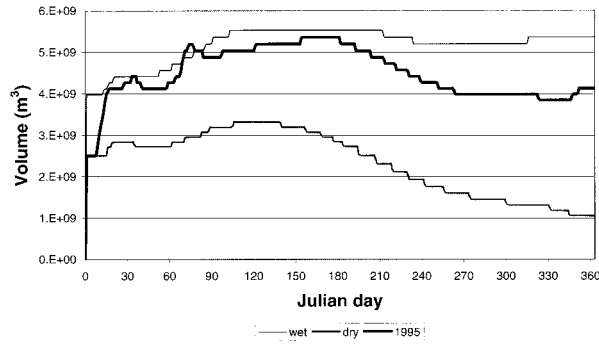


Figure 2. Lake volume under two hydrologic scenarios and in 1995.

We simulated three hydrologic and two operational scenarios (with and without the TCD operating) with the model: (a) hydrologically wet, (b) hydrologically dry, and (c) calendar year 1995 conditions (Figure 2). The hydrologically wet and dry scenarios were constructed from historical data, whereas the 1995 scenario demonstrated actual-year conditions. The 1995 calendar year was chosen because it was one of the years used to calibrate the model (Bartholow and others forthcoming). Simulations without the TCD operating incorporated release patterns to maximize hydropower for the wet and dry scenarios, and actual release patterns that used the bypass outlets for the 1995 conditions. Simulations with the TCD operating used the same input data as the corresponding without-TCD runs, except that release distributions used TCD outlets at one or more elevations that were changed on a daily basis in an attempt to meet a set of downstream temperature targets (Bartholow and others forthcoming). Because Bartholow and others (forthcoming) found that W2 performed better at predicting hypolimnetic or epilimnetic averages of algae than over the entire vertical profile, estimates of net algal production were summarized over the stratified period and across the whole lake and in the epilimnion for application with the food web model.

In W2, the change in algae concentration for each timestep and each model computational unit (cell) was calculated according to the following equation (Cole and Buchak 1995):

$$\frac{\partial \Phi_a}{\partial t} = K_{ag} \Phi_a - K_{ar} \Phi_a - K_{ae} \Phi_a - K_{am} \Phi_a - \frac{\omega_a}{\Delta z} \Phi_a \quad (2)$$

where

$$\Phi_a = \text{algal concentration (g ash-free dry mass [AFDM] m}^{-3}\text{)}$$

K_{ag} = algal growth rate (s^{-1})

K_{ar} = algal dark respiration rate (s^{-1})

K_{ae} = algal excretion rate (s^{-1})

K_{am} = algal mortality rate (s^{-1})

ω_a = algal settling rate ($m s^{-1}$)

Δz = cell thickness (m)

Because energy transfer was defined in terms of production (Eq. [1]), the total production available at the primary producer level (that is, trophic position 1) was defined as the net production or the gross production minus plant respiration (Goldman 1968; Begon and others 1996). We modified the model to report net algal production in grams of organic matter dry weight as:

$$\text{Net algal production} = (K_{ag} \Phi_a - K_{ar} \Phi_a) \Delta t V \quad (3)$$

where

Δt = length of time interval of output (s)

V = volume of cell (m^3)

For each of the six simulations, volume, gross production, dark respiration, and net production were output eight times per day (that is, $\Delta t = 10,800$ s) for both the entire reservoir and for the epilimnion. Cells were assigned to the epilimnion if they were above the computed thermocline for model segment 19, which was considered representative of the main lake area of the reservoir. The thermocline was defined as the highest point in the water column at which the water temperature differed from the surface water temperature by $1^\circ C$, and the stratified period was defined as a continuous period in which the thermocline was always less than 50 m deep (Bartholow and others forthcoming).

Daily values of the volume and productivity predictions were obtained by numerically integrating over each day using Simpson's 1/3 rule (Chapra and Canale 1988). The daily results of the without-TCD runs were subtracted from the corresponding results for the with-TCD runs to calculate the change in primary productivity due to the TCD. Changes in net algal production were then summed over the whole reservoir and for the epilimnetic region of the reservoir during the stratified period. This was the period in which the largest TCD-related changes in mixing patterns were expected to occur (Bartholow and others forthcoming). Result-

ing changes in thermal and nutrient patterns would then affect production and fish growth.

Food Web–Energy Transfer Model

One of our first tasks was to map the Shasta Lake food web. Very little was known about the structure of the food web at the start of our study. The California Department of Fish and Game (CDFG) prepared a fishery management plan that provided a species list (CDFG 1991), but no specific data on diets or biomasses of Shasta Lake fishes were available. Because construction of the TCD was complete and implementation was about to begin, a multi-year field study to document trophic structure was not possible. We therefore chose stable isotope analysis to estimate the configuration of the Shasta Lake food web. Stable isotope analysis was appealing because it provides insight into food web structure with minimal field sampling and has been used successfully for food web estimation in a number of freshwater environments (Estep and Vigg 1985; Hamilton and others 1992; Kling and others 1992; Angradi 1994; Yoshioka and others 1994; Gu and others 1996, 1997; Whitley and Rabeni 1997).

The fundamental concept behind the use of stable isotopes in trophic studies is that “you are what you eat.” Because stable isotopes incorporate two kinds of information (that is, origin and fractionation), the isotopic signature of an individual will reflect the signature of the sources of the isotopes (that is, where the isotopes first entered the food web) and the change in the isotopic signature due to isotopic fractionation by physical and chemical reactions as the isotopes are consumed and metabolized in the food web (Peterson and Fry 1987). Isotopes accumulate in body tissues over time, so a one-time analysis of stable isotopes provides a time-integrated measure of the diet (Fry and Sherr 1984; Hesslein and others 1993; Vander Zanden and others 1998). In addition, stable isotope analysis can be very useful for detecting omnivory in food webs because isotope signatures can be measured in all levels of the food web, including phytoplankton, zooplankton, and aquatic insects (Michener and Schell 1994; Vander Zanden and Rasmussen 1996; France 1997).

The most commonly measured stable isotope ratios in aquatic food web studies are the carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) ratios. There is a slight (0.2‰–1.1‰) enrichment of $\delta^{13}\text{C}$ in animals relative to their diet, which means that the $\delta^{13}\text{C}$ signature of the primary producer (first organic food source) is likely to be preserved through several trophic levels (Peterson and Fry 1987; Michener

and Schell 1994; Yoshioka and others 1994; France and Peters 1997). Thus, carbon isotope analysis can be used to identify primary food sources and distinguish the influence of different primary food sources if the isotopic signatures of those food sources are distinctive enough (Forsberg and others 1993; Michener and Schell 1994). The enrichment of $\delta^{15}\text{N}$ with trophic level is much greater than with carbon, with a characteristic gain of about 3‰–4‰ per trophic level (Michener and Schell 1994). Because of this phenomenon, the nitrogen isotope ratio has been used as an indicator of the trophic position of a consumer (Fry 1988; Kling and others 1992; Yoshioka and others 1994).

Sampling the food web. We selected a subset of 10 fish species (Table 1) from the 26 species reported to occur in Shasta Lake (CDFG 1991) for inclusion in our food web analysis. This subset included planktivorous, omnivorous, and piscivorous species, and species important to the sport fishery. Species that were considered rare (CDFG 1991) or were primarily benthivorous (for example, catfishes, carp, suckers) were not included because we assumed that they would not contribute significantly to pelagic energy pathways. Because all sizes of basses were abundant, and because basses undergo a trophic ontogeny (Gerking 1994; Vander Zanden and others 1998) in which prey selection varies from small invertebrate prey early in life to large, primarily fish prey later (Emig 1966b, 1966c; McKechnie 1966; Coble 1975; Moyle 1976), we subdivided basses into small (less than 113 mm total length [TL]), medium (114–290 mm TL), and large (more than 290 mm TL) size classes.

Invertebrate taxa of interest included zooplankton, crayfish, aquatic insects, and terrestrial insects. Because frequent water level fluctuations in the reservoir prevented any appreciable aquatic macrophyte growth (N. Manji, personal communication), the base of the Shasta Lake food web was assumed to consist of phytoplankton, periphyton, and detritus (assumed to be composed of material of both aquatic and terrestrial origin).

Sampling occurred in June and July 1998 at four locations throughout the reservoir: on the Pit River, the Sacramento River, and the McCloud River arms, and in the main body of Shasta Lake (Figure 1). Fish were collected using electrofishing, gill netting, trap netting, hook-and-line fishing, or hand-held nets. The insects were gathered using hand-held nets or by catching them by hand. Zooplankton were sampled by taking 30–0 meter vertical hauls with a 64- μm or a 500- μm Birge closing net.

We took dorsal muscle samples from all fish

Table 1. Fish, Invertebrate, and Plant Taxa of Shasta Lake Included in the Food Web Analysis

Taxon	Scientific Name	Code	Size Class
Chinook salmon	<i>Oncorhynchus tshawytscha</i>	CHS	320–538 mm TL
Brown trout	<i>Salmo trutta</i>	BRT	510 mm TL
Big bass	<i>Micropterus salmoides</i> and <i>M. punctulatus</i>	BBS	>290 mm TL
Medium smallmouth bass	<i>M. dolomieu</i>	MSMB	114–290 mm TL
Medium bass	<i>M. salmoides</i> and <i>M. punctulatus</i>	MBS	114–290 mm TL
Rainbow trout	<i>O. mykiss</i>	RBT	290–410 mm TL
Threadfin shad	<i>Dorosoma petenense</i>	TFS	All sizes
Small bass	<i>M. salmoides</i> and <i>M. punctulatus</i>	YC1BS	0–113 mm TL
Green sunfish	<i>Lepomis cyanellus</i>	GSF	83–125 mm TL
Sacramento pikeminnow	<i>Ptychocheilus grandis</i>	SQF	75–122 mm TL
Bluegill	<i>Lepomis macrochirus</i>	BLG	All sizes
Crayfish	Order <i>Decapoda</i>	CRA	All sizes
Zooplankton	Class <i>Branchiopoda</i>	ZOO	>64 µm
Terrestrial insects	—	TINS	All sizes
Aquatic insects	—	AINS	All sizes
Phytoplankton	—	PHY	—
Periphyton	—	PER	—
Detritus	—	DET	—

Fish size classes were chosen based on trophic ecology and sizes represented in our samples.

larger than 67 mm TL; for smaller fish (less than 67 mm), whole individuals were collected to ensure enough material for analysis. Although different body parts and tissues can exhibit different isotopic signatures, muscle tissue has an intermediate signature in most organisms (DeNiro and Epstein 1978, 1981; Tieszen and others 1983; Mizutani and others 1991). Recent laboratory work with rainbow trout showed that white muscle tissue was the most appropriate for ecotrophic studies (Pinnegar and Polunin 1999). Stomachs were removed from all Alabama spotted bass from which dorsal muscle tissue was taken; stomachs were also removed from a subset of larger bluegill. All stomachs were preserved with a 10% formalin solution.

Isotope measurements and construction of the aquatic food web. All tissue and whole body samples were dried for at least 24 h in a 60°C oven and then ground to a homogeneous powder using a mortar and pestle. To economize on mass spectrometer costs, individual fish samples were pooled into composite samples according to length classes that approximated age classes (N. Manji, personal communication; Moyle 1976) and reservoir locations for Alabama spotted bass, smallmouth bass, chinook salmon, rainbow trout, bluegill, green sunfish, Sacramento pikeminnow, and threadfin shad. Composite samples contained an equal mass of each individual sample. Carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope ratios were measured in a VG Isoch-

rom mass spectrometer with a Carlo-Erba NA1500 elemental analyzer. Mean standard errors of replicate carbon and nitrogen measurements were 0.1162‰ and 0.4789‰, respectively.

We used a general linear models approach to analyze the isotopic signatures of species and size classes that were collected at more than one location to determine if differences in mean carbon or nitrogen signatures were significant among locations. Both the carbon and nitrogen signatures were considerably higher for species collected in the Pit River arm compared to their counterparts in the other parts of the lake during both June and July 1998 ($P < 0.008$; α was adjusted for multiple comparisons). Intensive agriculture in the Pit River watershed may have accounted for the unusual isotopic values (Kendall 1998). Based on these results, the carbon and nitrogen signatures for the Main Lake, the Sacramento River arm, and the McCloud River arm were grouped together, and the signatures from the Pit River arm were not used in further analyses.

We did not measure phytoplankton signatures because they are known to be highly variable over time and space due to high turnover rates, changes in species composition over time (Kling and others 1992; Boon and Bunn 1994; Goericke and others 1994; France and others 1997; Gu and others 1997), and different nutrient sources (Kline and others 1990; France and others 1997; Keough and

others 1998). It is also difficult to measure phytoplankton signatures because samples are often contaminated with detrital material (Michener and Schell 1994; del Giorgio and France 1996; Riera and Richard 1996; France and others 1997). We therefore estimated phytoplankton signatures from the measured zooplankton signatures using a baseline signature approach (Vander Zanden and others 1997). This approach assumed that zooplankton consumed only phytoplankton and that because zooplankton are longer-lived, their signatures should reflect an integration of the variable phytoplankton signatures over time. Although zooplankton are known to consume other material in addition to phytoplankton, we assumed that phytoplankton was the predominant source of particulate organic matter and that phytoplankton signatures would be reflected in their consumers. Thus, phytoplankton signatures were estimated by subtracting the estimated trophic enrichment of carbon and nitrogen signatures from the corresponding measured zooplankton signatures. For example, the carbon signature for phytoplankton was estimated using the following equation:

$$\delta^{13}C'_{\text{phyto}} = \delta^{13}C_{\text{zoo}} - \Delta'_c \quad (4)$$

where

$\delta^{13}C'_{\text{phyto}}$ = estimated phytoplankton carbon signature (‰)

$\delta^{13}C_{\text{zoo}}$ = measured zooplankton carbon signature (‰)

Δ'_c = estimated trophic enrichment of carbon signature (‰)

A similar equation was used to estimate the nitrogen signature of phytoplankton (Saito 1999).

Periphyton and detritus signatures were also estimated with the baseline signature approach. We compiled reported carbon and nitrogen signatures for periphyton and detritus from 14 studies (Saito 1999), but base signatures vary greatly from place to place (Fry and Sherr 1984; France 1995a, 1995b; Cabana and Rasmussen 1996). Because differences between producers and consumers are highly replicable due to characteristic trophic enrichment (Coleman and Fry 1991; Lajtha and Michener 1994), we selected a subset of these studies that had food web components that coincided with components in the Shasta Lake food web. We replicated the literature-reported relationships between per-

iphyton and detritus signatures and these other food web components to estimate signatures at Shasta Lake. For example, Angradi (1994) reported carbon and nitrogen signatures for chironomids and *Cladophora* with epiphytes on the Colorado River. A periphyton carbon signature at Shasta was estimated using the carbon signature of the chironomids that were included in the Shasta Lake food web:

$$\begin{aligned} \delta^{13}C_{\text{periphyton, Shasta}} &= \delta^{13}C_{\text{chironomid, Shasta}} \\ &- (\delta^{13}C_{\text{chironomid, Angradi (1994)}} - \delta^{13}C_{\text{epiphytes, Angradi (1994)}}) \end{aligned} \quad (5)$$

where

$\delta^{13}C_{\text{periphyton, Shasta}}$ = estimated periphyton carbon signature (‰)

$\delta^{13}C_{\text{chironomid, Shasta}}$ = measured chironomid carbon signature at Shasta (‰)

$\delta^{13}C_{\text{chironomid, Angradi (1994)}}$ = measured chironomid carbon signature in Angradi (1994) (‰)

$\delta^{13}C_{\text{epiphytes, Angradi (1994)}}$ = measured *Cladophora* with epiphytes carbon signature in Angradi (1994) (‰)

Similar comparisons were made with published data from other studies for both carbon and nitrogen signatures for periphyton and detritus. The averages of these comparisons were used as the signatures in the Shasta Lake food web.

Estimations of diet, trophic position, energy transfer, and phytoplankton dependency. The carbon and nitrogen signatures of each consumer were estimated based on the proportions of consumed species in its diet:

$$\delta^{13}C'_i = \sum_{j=1}^n [f'_{ij}(\delta^{13}C_j + \Delta'_c)] \quad (6)$$

$$\delta^{15}N'_i = \sum_{j=1}^n [f'_{ij}(\delta^{15}N_j + \Delta'_n)] \quad (7)$$

$$\sum_{j=1}^n f'_{ij} = 1 \quad (8)$$

where

$\delta^{13}C'_i$ = estimated carbon signature
of consumer i (‰)

$\delta^{15}N'_i$ = estimated nitrogen signature
of consumer i (‰)

$\delta^{13}C_j$ = measured carbon signature
of prey j (‰)

$\delta^{15}N_j$ = measured nitrogen signature
of prey j (‰)

Δ'_C = estimated trophic enrichment of
carbon signature (‰)

Δ'_N = estimated trophic enrichment of
nitrogen signature (‰)

f'_{ij} = estimated fraction of diet of
consumer i that is prey j

n = total number of prey in diet of
consumer i

Eq. (8) assumed that all possible food sources for each consumer had been included in the analysis. Diet rules were established that set corresponding f_{ij} values to zero if a consumer was assumed not to consume a particular prey. These rules (Table 2) were established from a literature review of 40 studies (Saito 1999). We corroborated the literature review diets with results of stomach analyses on bluegill and Alabama spotted bass from Shasta Lake.

We used an optimization procedure (the Solver module in Microsoft Excel) to estimate the diet proportions of all food web components simultaneously by minimizing the sum of squares of the differences between the estimated signatures and the measured signatures. For the optimization, all proportions of diet were initially set to zero, and the estimated enrichments in signature per trophic level (Δ') were 0.0‰ for both carbon and nitrogen. These values changed independently during the optimization iterations. We performed a sensitivity analysis of the Solver settings for the optimization procedure to ensure that the procedure was reproducible and appropriate for our application.

The optimization procedure required two additional constraints that limited the amount of phytoplankton consumed by bluegill and crayfish (5%

and 15% maximum allowable in diet, respectively) beyond the diet rules in Table 2. These constraints were needed because without them, the optimization procedure resulted in the diets of bluegill and crayfish consisting largely of phytoplankton. Although bluegill and crayfish are known to consume phytoplankton (Emig 1966a; Siefert 1972; Moyle 1976; Hobbs 1991), it is unlikely that this food source comprised a large fraction of their diets.

The trophic position of each taxon in Table 1 was estimated using the approach of Levine (1980), Vander Zanden and others (1997), and Vander Zanden and Rasmussen (1996):

$$TP'_i = \sum_{j=1}^n (a_{ij}TP_j + 1) \quad (9)$$

where

TP'_i = estimated trophic position of consumer i

a_{ij} = proportion of diet of consumer i due

to prey j

TP_j = trophic position of prey j

n = total number of prey in diet of consumer i

This approach allowed us to calculate trophic position on a continuous scale rather than at discrete trophic levels. Trophic position is more realistic because of the high degree of omnivory that is present in aquatic food webs (Kling and others 1992; Vander Zanden and Rasmussen 1996; Vander Zanden and others 1997).

Phytoplankton, periphyton, and detritus were assumed to occupy trophic position 1. Zooplankton and aquatic and terrestrial insects were assumed to occupy trophic position 2, and their diets were not estimated with the Solver algorithm.

Consumers' dependence on phytoplankton could be calculated using the approach of Christensen and Pauly (1993). However, the lack of available biomass, production/biomass, and energy flux data for the Shasta Lake food web made the application of such an approach very difficult. Instead, we used a bottom-up approach and applied the assumed 10% trophic transfer efficiency (Eq. [1]) through pathways linked to the phytoplankton to estimate the energy transferred to consumers, ET_i . Consumers at higher computed trophic positions necessarily had more trophic transfers to obtain phytoplankton energy than those at lower trophic positions. Thus,

inferences about consumers' relative energy dependence on phytoplankton can be made only for consumers with similar trophic positions.

To test the sensitivity of our conclusions about energy transfer to our 10% transfer efficiency assumption, we calculated energy transfer efficiencies from the phytoplankton for each consumer using the trophic pathways linked to phytoplankton, assuming (a) 10% transfer efficiencies for all trophic transfers, (b) varying transfer efficiencies by trophic level using average transfer efficiencies from Christensen and Pauly (1993) (that is, 10.0% from trophic level 1 to trophic level 2, 11.0% from trophic level 2 to 3, 8.5% from trophic level 3 to 4, 7.5% from trophic level 4 to 5, 9.0% from trophic level 5 to 6, and 9.2% for all other trophic transfers), (c) decreasing all transfer efficiencies by 10% (that is, using 9% transfer efficiencies for all trophic transfers), and (d) increasing all transfer efficiencies by 10% (that is, using 11% transfer efficiencies for all trophic transfers).

Linking the Water Quality Model to the Food Web–Energy Transfer Model

To convert the net algal production from mass to energy units, a factor of 21,265 J per gram (g) AFDM was applied to the changes in net production that were predicted by W2. This factor was determined by averaging energy densities (Cummins and Wuycheck 1971) for algae species found at Shasta (Lieberman and Horn 1998).

The estimated energy available due to phytoplankton net production during the stratified period was used to estimate the wet biomass of fish that could be supported by using the following equation:

$$\text{Biomass}_i = \Delta E_{\text{phyto}} \frac{ET_i}{ED_i} \quad (10)$$

where

Biomass_i = estimated wet biomass of
taxon i (g)

ΔE_{phyto} = change in energy due to
phytoplankton net production (J)

ET_i = energy transfer coefficient from
phytoplankton to taxon i

ED_i = energy density of taxon i (J g^{-1}),
(Hanson and others 1997)

We also estimated the connectance of consumers to phytoplankton as a primary organic food source by the approach of Harrigan and others (1989). The measured signatures for each species were used to estimate the combined signature of primary organic food sources by back-calculating with the trophic enrichments and continuous trophic positions estimated using Eq. (9). For example, the estimated carbon signature of all combined primary organic sources for consumer i ($\delta^{13}C'_{\text{prim}, i}$) was calculated according to the following equation:

$$\delta^{13}C'_{\text{prim}, i} = \delta^{13}C_i - (TL_i - 1)\Delta'_C \quad (11)$$

where

$\delta^{13}C'_{\text{prim}, i}$ = estimated carbon signature of all
combined primary organic
sources for consumer i (‰)

$\delta^{13}C_i$ = measured carbon signature for
consumer i (‰)

TL_i = estimated trophic level for consumer i

Δ'_C = estimated trophic enrichment of carbon
signature from Excel Solver (‰)

Similar calculations were made to estimate the nitrogen signature of all the combined primary organic sources for consumer i ($\delta^{15}N'_{\text{prim}, i}$). The primary organic source signatures of each consumer were estimated according to the following three-source mass balances (Harrigan and others 1989):

$$\delta^{13}C''_{\text{prim}, i} = f_{\text{phyto}, i}(\delta^{13}C'_{\text{phyto}}) + f_{\text{peri}, i}(\delta^{13}C'_{\text{peri}}) + f_{\text{det}, i}(\delta^{13}C'_{\text{det}}) \quad (12)$$

$$\delta^{15}N''_{\text{prim}, i} = f_{\text{phyto}, i}(\delta^{15}N'_{\text{phyto}}) + f_{\text{peri}, i}(\delta^{15}N'_{\text{peri}}) + f_{\text{det}, i}(\delta^{15}N'_{\text{det}}) \quad (13)$$

$$f_{\text{phyto}, i} + f_{\text{peri}, i} + f_{\text{det}, i} = 1 \quad (14)$$

where

$\delta^{13}C''_{\text{prim}, i}$ = estimated carbon signature of
primary organic sources for consumer i (‰)

$\delta^{15}N''_{\text{prim}, i}$ = estimated nitrogen signature of
primary organic sources for consumer i (‰)

$\delta^{13}C'_{\text{phyto}}$ = estimated carbon signature
of phytoplankton (‰)

$\delta^{15}N'_{\text{phyto}}$ = estimated nitrogen signature
of phytoplankton (‰)

$\delta^{13}C'_{\text{peri}}$ = estimated carbon signature of
periphyton (‰)

$\delta^{15}N'_{\text{peri}}$ = estimated nitrogen signature of
periphyton (‰)

$\delta^{13}C'_{\text{det}}$ = estimated carbon signature
of detritus (‰)

$\delta^{15}N'_{\text{det}}$ = estimated nitrogen signature
of detritus (‰)

$f'_{\text{phyto}, i}$ = estimated fraction of diet of
consumer i that is phytoplankton

$f'_{\text{peri}, i}$ = estimated fraction of diet of
consumer i that is periphyton

$f'_{\text{det}, i}$ = estimated fraction of diet of
consumer i that is detritus

These equations were solved simultaneously in the same manner used to solve Eqs. (6), (7), and (8). Results of this analysis can be compared between species regardless of trophic position because of the back-calculation to the signature of all primary organic food sources (Eq. [11]).

RESULTS

When the TCD was operating, hydrologically wet conditions resulted in increases in net production over the stratified period, whereas hydrologically dry conditions resulted in decreased net production (Figure 3). The results for 1995 showed an overall increase in net production in the whole lake with the TCD operating, but only a very slight increase in epilimnetic net production. In fact, all scenarios showed that hypolimnetic net production increased with TCD operation. Gains in the whole lake were greater than gains in the epilimnion during the wet and 1995 scenarios, and the losses in the whole lake were less than losses in the epilimnion during the dry scenario. The increased hypolimnetic net algal

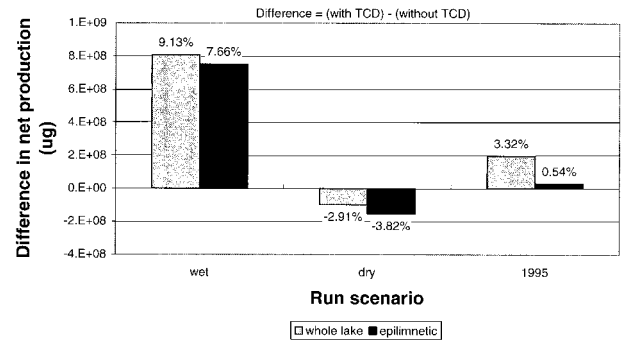


Figure 3. Difference in net phytoplankton production over stratified period (ΔE_{phyto}) as predicted by CE-QUAL-W2.

production could be due to warmer hypolimnetic temperatures and increased mixing. Hanna and others (1999) showed that hypolimnetic water temperatures were warmer later in the year with TCD operation, and these warmer temperatures could cause the model to predict increased hypolimnetic algal production during the stratified period.

The 300+ individual samples collected during the field sampling were analyzed for their carbon and nitrogen isotope signatures, with over half of them pooled into composite samples. Using statistical analyses performed with SAS System Release 6.11 (SAS Institute Inc., Cary, NC, USA), we determined that composite signatures were representative of the mean of the individual signatures for both carbon and nitrogen (one-way ANOVA: $n = 12$; $P > 0.57$).

Estimated carbon signatures for periphyton and detritus based on 11 previous freshwater studies had relatively little variation and averaged to -26.51‰ and -28.04‰ , respectively (Tables 3 and 4). Estimated nitrogen signatures (averages of 2.94‰ for periphyton and -1.18‰ for detritus) showed much greater variation.

The average estimated periphyton and detritus signatures were used with the estimated phytoplankton signatures to determine the signatures of consumers using the optimization procedure (Figure 4 and Table 5). The estimated signatures compared favorably to measured signatures, with an overall mean squared error 4.12‰ for both carbon and nitrogen. Sensitivity analysis of the optimization procedure indicated that the method was robust as long as the precision with which the value of a constraint cell met a target was set high enough, and the automatic scaling option in Solver was not used when inputs and outputs had large differences in magnitude.

Table 3. Comparisons Used to Estimate Periphyton Carbon and Nitrogen Signatures at Shasta Lake

Reference (yr)	Location	Estimated Signatures		Shasta Species Used
		$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	
Angradi (1994)	1–2 km downstream of Glen Canyon Dam on Colorado River	–29.50	—	Chironomids
Angradi (1994)	1–2 km downstream of Glen Canyon Dam on Colorado River	–34.13	10.87	Rainbow trout
Bunn and others (1989)	Alik Lake, Quebec	–24.60	—	Chironomids
Bunn and others (1989)	Alik Lake, Quebec	–16.57	—	Tipula
Estep and Vigg (1985)	Pyramid Lake, NV	–28.30	—	Chironomids
Fry (1991a)	Hubbard Brook, Mirror Lake, NH	–23.72	–0.37	Crayfish
Fry (1991a)	Hubbard Brook, Mirror Lake, NH	–18.31	–0.24	Medium smallmouth bass
Fry (1991a)	Konza Prairie, KS	–32.41	4.32	Mayfly
Gu and others (1997)	Smith Lake, AK	–32.60	—	Chironomids
Gu and others (1997)	Smith Lake, AK	–28.92	4.68	Mayfly
Hecky and Hesslein (1995)	Canadian Shield lake	–22.25	1.04	Crayfish
Junger and Planas (1994)	Laflamme Creek just downstream of Lac Laflamme, Quebec	–27.60	—	Chironomids
Junger and Planas (1994)	De l'Aqueduc Creek, Quebec	–27.85	—	Chironomids
Peterson and others (1993)	Tundra river ecosystem (control)	–32.7	—	Chironomids
Peterson and others (1993)	Tundra river ecosystem (control)	–21.42	0.28	Mayfly
Rau (1980)	Lake Findlay, WA	–23.30	—	Chironomids
Average		–26.51	2.94	
Coefficient of variation		–0.20	1.39	

The estimated consumer diets resulting from the optimization procedure were used to trace food web pathways originating from phytoplankton (Figure 5). For example, zooplankton ate 100% phytoplankton, which resulted in one pathway: phytoplankton → zooplankton. Threadfin shad ate 65% zooplankton and 35% aquatic insects. This also resulted in one pathway to phytoplankton (for all consumers, aquatic and terrestrial insects, periphyton, and detritus were assumed to have no trophic linkage with phytoplankton): phytoplankton → zooplankton → threadfin shad.

Only one species group (medium bass 114–290 mm TL) was estimated by the analysis as being cannibalistic. We assumed that the cannibalism involved larger bass eating smaller ones in this size group, so only one iteration of cannibalism was modeled. In other words, cannibalism was represented in the food web by having the medium bass eat medium bass that had eaten everything from the diet analysis results except other medium bass. In all, the diet proportions estimated from isotope analysis resulted in 398 trophic pathways linked to phytoplankton.

The trophic position calculations indicated that chinook salmon were the top predators in the

Shasta Lake food web (Table 6). Higher predator species such as big bass, brown trout, medium smallmouth bass, and rainbow trout had similar trophic positions, whereas bluegill occupied the lowest trophic position of modeled consumers. Intermediate prey species such as threadfin shad, year class 1 bass, green sunfish, and Sacramento pikeminnow occupied similar trophic positions about one full position below the higher predator species.

The relative differences in phytoplankton transfer efficiencies between consumers were similar regardless of the trophic transfer efficiency assumption made (Figure 6), so predicted changes in consumer biomass were made using energy transfer coefficients that assumed 10% transfer efficiencies for all trophic transfers (Table 6). Evaluation of these energy transfer coefficients indicated that rainbow trout, Sacramento pikeminnow, and green sunfish were minimally connected to phytoplankton, if at all. Instead, these species were predicted to eat diets dominated by aquatic and terrestrial insects, which were likely supported by terrestrial primary productivity.

Table 4. Comparisons Used to Estimate Detritus Carbon and Nitrogen Signatures at Shasta Lake

Reference (yr)	Location	Estimated Signatures		Shasta Species Used
		$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	
Angradi (1994)	1–2 km downstream of Glen Canyon Dam on Colorado River	-23.60	—	Chironomids
Angradi (1994)	1–2 km downstream of Glen Canyon Dam on Colorado River	-28.23	7.56	Rainbow trout
Bunn and others (1989)	Alik Lake, Quebec	-33.30	—	Chironomids
Bunn and others (1989)	Alik Lake, Quebec	-25.27	—	Tipula
Estep and Vigg (1985)	Pyramid Lake, NV	-28.30	—	Chironomids
Fry (1991a)	Konza Prairie, KS	-34.21	4.05	Crayfish
Fry (1986)	Green Lake, NY	-28.89	—	Crayfish
Gu and others (1997)	Smith Lake, AK	-28.40	—	Chironomids
Gu and others (1997)	Smith Lake, AK	-29.80	—	Chironomids
Gu and others (1997)	Smith Lake, AK	-24.72	-1.62	Mayfly
Gu and others (1997)	Smith Lake, AK	-26.12	-5.12	Mayfly
Harrington and others (1998)	Bingo Brook, VT	—	-0.90	Mayfly
Harrington and others (1998)	West Branch, VT	—	-1.20	Mayfly
Harrington and others (1998)	Bethel–Gilead tributary, VT	—	-2.72	Mayfly
Harrington and others (1998)	Peavine tributary, VT	—	-0.05	Mayfly
Harrington and others (1998)	First Branch, VT	—	-4.80	Mayfly
Harrington and others (1998)	Third Branch, VT	—	-6.99	Mayfly
Rau (1980)	Lake Findlay, WA	-26.00	—	Chironomids
Average		-28.04	-1.18	
Coefficient of variation		-0.11	-3.50	

The alternative calculations using the approach of Harrigan and others (1989) resulted in the estimation of almost half or more of the primary organic source being derived from phytoplankton for small bass, threadfin shad, and crayfish (Table 6). The constraints of Eq. (11) in the approach of Harrigan and others (1989) were not satisfied for rainbow trout, green sunfish, and terrestrial and aquatic insects in the final solution; however, none of these species were expected to be connected to the phytoplankton. Both the energy transfer coefficient calculations and the approach of Harrigan and others (1989) indicated that rainbow trout and green sunfish were expected to be minimally affected by changes in phytoplankton abundance due to TCD operation relative to bass species (Table 6). These taxa were therefore not included in the analysis of biomass changes.

Application of energy transfer and energy density coefficients to the net algal production estimates resulted in predictions of gains in species wet weight due to TCD operations under hydrologically wet conditions and losses in wet weight under dry conditions. Comparison of the relative changes in consumer biomass normalized by changes in phytoplankton pro-

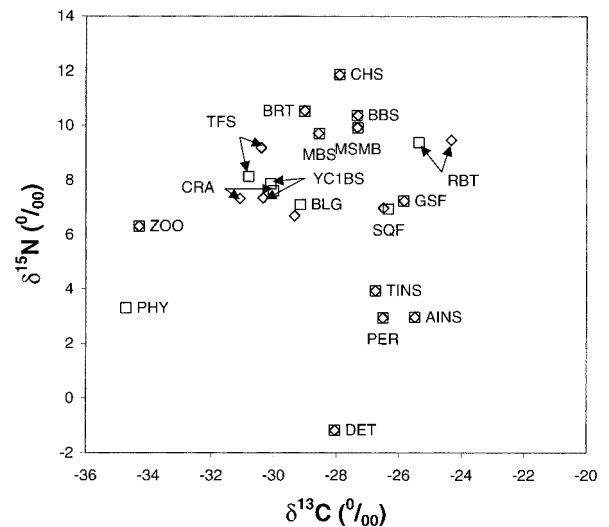


Figure 4. Measured and estimated signatures for Shasta Lake grouped species. Measured signatures are indicated with a \diamond ; estimated signatures are indicated with a \square . Refer to Table 1 for codes.

duction (Table 6) indicate that among predators, bass species are the most sensitive to changes in phytoplankton abundance.

Table 5. Measured and Estimated Carbon and Nitrogen Signatures and Estimated Trophic Positions of Consumers, Producers, and Detritus from Shasta Lake

Code	$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)				Estimated trophic position
	Measured range	<i>n</i>	Avg.	Estimated	Measured range	<i>n</i>	Avg.	Estimated	
CHS	-28.22 to -27.60	2	-27.91	-27.91	11.60 to 12.10	2	11.85	11.86	4.4
BRT	-29.02	1	-29.02	-29.02	10.54	1	10.54	10.52	3.9
BBS	-28.70 to -25.86	6	-27.32	-27.35	9.87 to 11.33	6	10.37	10.37	4.0
MSMB	-27.69 to -26.99	2	-27.34	-27.32	9.71 to 10.13	2	9.92	9.91	3.9
MBS	-29.44 to -27.88	9	-28.58	-28.56	9.03 to 10.52	9	9.71	9.70	3.7
RBT	-24.33	1	-24.33	-25.36	9.46	1	9.46	9.38	3.9
TFS	-29.94 to -31.21	3	-30.41	-30.81	8.92 to 9.67	3	9.18	8.13	3.0
YC1BS	-32.01 to -27.23	9	-30.35	-30.11	5.74 to 8.69	9	7.34	7.86	3.0
CRA	-31.09	1	-31.09	-30.02	7.32	1	7.32	7.60	3.2
GSF	-26.17 to -25.49	3	-25.84	-25.85	6.74 to 7.51	3	7.23	7.23	3.1
SQF	-27.33 to -25.67	2	-26.50	-26.34	6.45 to 7.49	2	6.97	6.94	3.0
BLG	-32.11 to -24.55	7	-29.34	-29.16	5.81 to 7.19	7	6.69	7.10	2.3
ZOO ^a	-35.43 to -32.52	5	-34.31	-34.31	5.69 to 6.97	5	6.30	6.30	2.0
TINS ^a	-29.01 to -24.59	4	-26.75	-26.75	2.79 to 5.77	4	3.94	3.94	2.0
AINS ^a	-27.41 to -22.52	6	-25.49	-25.49	1.68 to 4.52	4	2.96	2.96	2.0
PHY ^{a,b}	nm		-34.72	-34.72	nm		3.30	3.30	1.0
PER ^{a,c}	nm		-26.51	-26.51	nm		2.94	2.94	1.0
DET ^{a,c}	nm		-28.05	-28.05	nm		-1.18	-1.18	1.0

nm, not measured

^aThese signatures and trophic levels were not estimated using Solver.

^bPhytoplankton signature was calculated from the zooplankton-measured signature according to the estimated changes in signature per trophic level.

^cSignatures for periphyton and detritus were estimated from literature review.

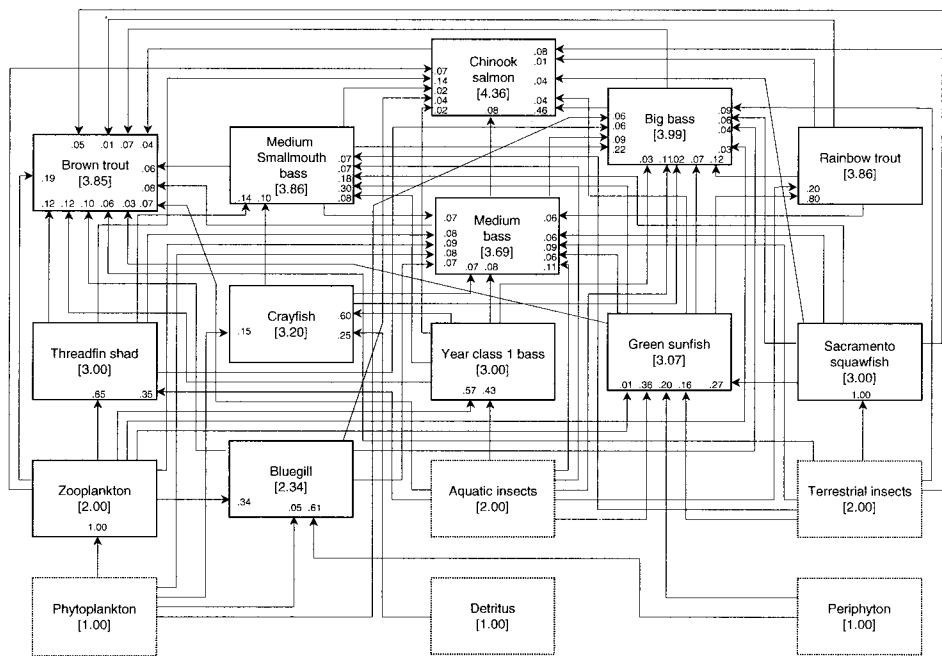


Figure 5. Estimated food web structure for Shasta Lake based on stable isotope analysis.

DISCUSSION

Stable isotope analysis provided an efficient and comprehensive means of estimating the Shasta Lake food web with minimal sampling and back-

ground data. Because isotopic signatures of consumers reflect time-integrated diet composition, and because muscle tissue has a half-time metabolic replacement of over 1 year (Hesslein and others 1993), a single sample in time provides a wealth of

Table 6. Consumer Trophic Position, Consumer Energy Transfer Coefficients, Fraction of Primary Organic Source Derived from Phytoplankton, Consumer Energy Densities, and Change in Consumer Biomass Relative to Phytoplankton Due to TCD Operations

Consumers	Trophic Position	Energy Transfer Coefficient, ET_i^a	Primary Organic Source Fraction Derived from Phytoplankton ^b	ED_i ($J g^{-1}$)	Change in Consumer Biomass ($g [g \text{ phytoplankton}]^{-1}$)
Zooplankton	2.0	0.1000	1.00	2514 ^c	0.8460
Bluegill	2.3	0.0084	0.39	4186 ^c	0.0427
Sacramento pikeminnow	3.0	— ^d	0.01	— ^d	— ^d
Year class 1 bass	3.0	0.0057	0.49	4186 ^c	0.0290
Threadfin shad	3.0	0.0065	0.58	6200 ^e	0.0223
Green sunfish	3.1	0.0001	0.00	4186 ^f	0.0005
Crayfish	3.2	0.0153	0.54	4512 ^g	0.0721
Medium bass	3.7	0.0092	0.32	4186 ^c	0.0467
Rainbow trout	3.9	— ^d	0.00	— ^d	— ^d
Medium smallmouth bass	3.9	0.0003	0.17	4186 ^c	0.0015
Brown trout	3.9	0.0023	0.40	6059 ^h	0.0063
Big bass	4.0	0.0065	0.18	4186 ^c	0.0330
Chinook salmon	4.4	0.0012	0.28	7736 ⁱ	0.0042

^aCalculated by applying Eq. (1) along food web pathways.
^bCalculated using the approach of Harrigan and others (1989).
^cEnergy density values from Hanson and others (1997).
^dSacramento pikeminnow and rainbow trout were not energetically connected to the phytoplankton.
^ePierce and others (1980).
^fEnergy density for green sunfish assumed to be same as for bluegill.
^gEnergy density value from Cummins and Wuycheck (1971).
^hEnergy density calculated as in Hanson and others (1997) for 299-g fish.
ⁱEnergy density calculated as in Hanson and others (1997) for 2000-g fish.

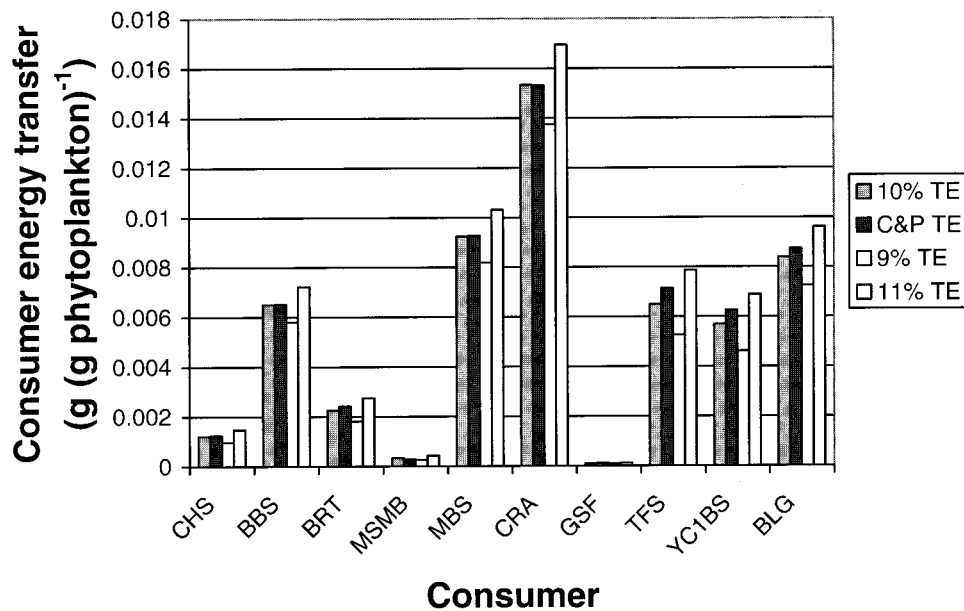


Figure 6. Consumer energy transfer coefficients ($g [g \text{ phytoplankton}]^{-1}$) assuming 10% transfer efficiencies for all trophic transfers (10% TE), varying transfer efficiencies by trophic level according to Christensen and Pauly (1993) (C&P TE), 9% transfer efficiencies for all trophic transfers (9% TE), and 11% transfer efficiencies for all trophic transfers (11% TE).

trophic information. Isotope analysis allowed us to uncover trophic linkages among predators and multiple prey, estimate trophic position of each consumer, and trace carbon sources for each consumer back to aquatic and terrestrial producers.

The use of stable isotope analysis to construct the food web–energy transfer model did involve some important assumptions. First, our approach assumed that all relevant pathways in the food web were accounted for and appropriately enabled (that

is, $f_i \geq 0$ for all possible items that can be consumed). This required that the occurrences of diet items from the literature review were appropriate for Shasta Lake's consumers and also that all components of the food web were represented in our sampling. With the exception of rainbow trout, threadfin shad, and crayfish, estimated isotopic signatures matched well with measured signatures. This suggests that our sampling of the food web captured the important components, and the resulting estimates of diet composition derived from prey isotopic signatures are tenable.

We also assumed that the enrichment of the carbon and nitrogen signatures (Δ') was constant throughout the food web. In other words, the amount of enrichment did not depend on predator or prey. Some studies have shown that the efficiency of assimilation of dietary components varies with species (Gannes and others 1997), possibly due to variation in lipid content between animals (Kling and others 1992; France 1995c; Focken and Becker 1998), different rates of fish growth (Hesslein and others 1993), or nutritional stress (Hobson and Clark 1992; Gannes and others 1997). Hobson and others (1995) observed greater carbon signature enrichment at lower trophic levels than at higher ones, which could be an indication of strong microbial loop influences or inconsistent fractionation processes with different trophic linkages. Further, Hobson and others (1999) found that terrestrial animals that consume both plants and animals tended to have isotopic signatures that were biased toward the animal food source. However, our analysis predicted an enrichment of 0.41‰ and 3.0‰ for carbon and nitrogen, respectively, which was encouraging because both of these values are well within the range of enrichment observed in other freshwater pelagic environments (Fry 1991b; France and Peters 1997).

When the stable isotope analysis was combined with a simple set of diet rules, the optimization procedure we used estimated not only trophic links but also the relative importance of various prey in the diet of each consumer. The approach therefore gave insights into interaction strength rather than a simple description of trophic links (Paine 1988). When we applied fundamental concepts about energy flow in ecosystems (Lindeman 1942; Pauly and Christensen 1995), a trophic transfer efficiency at each link enabled us to track energy flow through the ecosystem originating from phytoplankton.

Consumers in our food web–energy transfer model were not confined to a particular trophic level, but rather occupied a more realistic trophic position (Levine 1980; Vander Zanden and Rasmus-

sen 1996; Vander Zanden and others 1997) estimated from their degree of omnivory suggested by the isotope analysis. This analysis suggested extremely high connectivity (398 food chains linked to phytoplankton) within the Shasta Lake food web and widespread omnivory. Although this structure is consistent with contemporary thinking about the importance of omnivory in aquatic food webs (Polis 1994; Vander Zanden and Rasmussen 1996; France 1997), the food web–energy transfer model was a process-functional method concerned with energy flows and was not dynamic. Interspecific and intraspecific competition, and the interaction of productivity and consumption were therefore not addressed, although these dynamics are known to affect food consumption by fish and food web dynamics (Gerking 1994; DeAngelis and others 1996; Persson and others 1996). Because the food web model was not dynamic, diet proportions could not be adjusted based on changes in food abundance. Therefore, forecasting with the estimated linkages of consumers to phytoplankton relied on the assumption that no diet shifts occurred in response to changes in phytoplankton abundance. Although such dynamic behavior of consumers could be incorporated into our modeling framework, the necessary theory is not well developed (DeAngelis and others 1996; Osenberg and Mittelbach 1996).

When the food web–energy transfer model was coupled with phytoplankton predictions from the W2 model, we were able to estimate the relative bottom-up effects of new dam operations on various fish species. Until our W2 model can be adequately validated with additional field data, our predictions of the effects of the TCD on phytoplankton production are tentative. However, the conclusions of two recent limnological studies (Brett and others 1998; Lieberman and Horn 1998) generally agreed with W2 model simulations of phytoplankton production. Spring and fall peaks of algal biomass were observed in both studies and were also predicted by W2. The model predicted slight changes in phytoplankton production resulting from the TCD. Although some consumers were estimated to be much more sensitive to perturbations to phytoplankton supply than others (for example, bass and rainbow trout, respectively), the linked modeling predicted that fish biomass was generally unaffected by the new dam operations.

Because both of the limnological studies spanned only 2 years without the TCD operating and 1 year with the TCD operating, the observations of phytoplankton production were inconclusive about the effects of TCD operation (Brett and others 1998; Lieberman and Horn 1998). As Johnson (1998)

noted, small sample sizes in most ecological analyses make it difficult to distinguish natural from impact-induced variability. Conclusions from both our study and Bartholow and others (forthcoming) suggested that the observed variability in water quality and biological parameters in the limnological studies could be due largely to hydrologic and climate differences between study years rather than TCD operation. Thus, the modeling approach gave managers a tool to assess the relative effects of operational regimes long before they could be uncovered by monitoring the ecosystem under a variety of unplanned environmental conditions.

Our study showed that models are essential tools for addressing environmental issues such as the sensitivity of ecosystem components to changes in management policy (Christensen and others 1996). Increasing public understanding of solutions to mitigate the effects of large dams on riverine biodiversity is both a challenge and an opportunity for learning. Predicting reservoir impacts of new dam operations is challenging because of complex linkages among physical, chemical, and biological processes. Field studies to measure these impacts can lack statistical power because of high natural variability and the typical short duration of those studies. Experiments could give us stronger inference, but manipulations are constrained by socioeconomic factors, and replication and controls are usually lacking. Modeling can be an efficient approach to learning because it offers the advantage of control of nuisance variables, and it is unhindered by the duration or intensity of hypothetical manipulations. Models are also essential for summarizing knowledge and uncovering uncertainties, which are necessary steps to managing ecosystems adaptively.

We view our model constructs and their predictions as a set of hypotheses about the structure and function of the reservoir ecosystem that managers will have the opportunity to evaluate and refine as the effects of new dam operations are studied. Specifically, additional sampling and stable isotope analysis to estimate baseline isotopic signatures of producers and both aquatic and terrestrial primary consumers would reduce uncertainties in isotope-predicted diets of higher-level consumers. Phytoplankton predictions from W2 could also be validated with field measurements in years with different hydrologic characteristics. Alternatively, a more specific phytoplankton model (Chapra 1997) could have improved phytoplankton predictions. Although our models required many assumptions because of uncertainties about the system, some of our conclusions should be quite robust. For exam-

ple, the approach allowed us to determine that hydrologic influences may have more important ecosystem impacts than the effects of withdrawal elevations at Shasta Lake; it also allowed us to identify those species of fish that should be most sensitive to dam-induced perturbations of the phytoplankton supply.

Several researchers have advocated linked modeling approaches in aquatic ecosystem modeling (DeAngelis and Cushman 1990; Crockett 1994), and our linked models have demonstrated that interdisciplinary efforts can enhance the value of information obtained from studies of managed ecosystems. The approach exploited the strengths of engineering and ecological modeling methods and perspectives to address concerns that neither of the models could have addressed alone: (a) CEQUAL-W2 could not have addressed quantitatively the possible impacts to fish, and (b) the food web model could not have examined how phytoplankton availability might change due to reservoir operations. We are heartened by the application of stable isotopes analysis that allowed us to rapidly parameterize a food web–energy transfer model in the face of urgency of managers to implement new management regimes for the benefit of endangered species downstream. Linking this model with a well-developed water quality model then allowed us to translate limnological effects of new dam operations to potential impacts on resources of widespread management and public concern (for instance, fisheries). We believe the approach is valuable for the evaluation of TCDs, which is important because such structures are being considered for many other dams, including Glen Canyon Dam directly upstream of the Grand Canyon.

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