

Efficiencies of benthic and pelagic trophic pathways in a subalpine lake

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Abstract: Although the study of lakes has traditionally focused on pelagic production pathways, recent stable isotope and diet evidence indicates that benthic algal production is an important contributor to fish production. This has led to the suggestion that energy may be more efficiently passed along benthic food chains relative to their pelagic counterparts. To test this idea, we combined stable isotope based assessments of energy flow pathways with estimates of pelagic- and benthic-based primary and secondary production in Castle Lake, California. Approximately 50% of whole-lake primary production and 30% of whole-lake secondary production occurred in benthic habitats. Stable carbon isotopes and dietary data indicated that fish were predominantly supported by benthic (63%) and terrestrial (24%) secondary production. Ecological efficiencies (algal production / invertebrate production) were low in Castle Lake (<3%), though zoobenthic production was more efficiently passed to fish than was zooplankton production. The larger size of benthic prey relative to pelagic prey may affect fish prey selection and foraging efficiency, resulting in differences in ecological efficiency between pelagic and benthic trophic pathways.

Résumé : Alors que l'étude des lacs s'est traditionnellement concentrée sur les voies de production pélagiques, des données récentes provenant d'études des isotopes stables et des régimes alimentaires indiquent que la production des algues benthiques contribue de façon substantielle à la production de poissons. En conséquence, on a suggéré que l'énergie peut être transmise plus efficacement par les chaînes trophiques benthiques que par les chaînes pélagiques correspondantes. Afin de vérifier cette proposition, nous combinons des évaluations des voies du flux énergétique faites à l'aide d'isotopes stables avec des estimations des productions primaire et secondaire, tant pélagique que benthique, au lac Castle, Californie. Environ 50 % de la production primaire du lac entier et 30 % de la production secondaire du lac entier se réalisent dans les habitats benthiques. Les données d'isotopes stables de carbone et les analyses des régimes alimentaires indiquent que les poissons sont surtout alimentés par la production secondaire du benthos (63 %) et du milieu terrestre (24 %). Les efficacités écologiques (production des algues / production des invertébrés) sont faibles au lac Castle (<3 %), bien que la production du zoobenthos soit transmise plus efficacement aux poissons que celle du zooplancton. La taille plus grande des proies benthiques par rapport aux proies pélagiques peut affecter la sélection des proies et l'efficacité de l'alimentation chez les poissons, ce qui entraîne des différences d'efficacité écologique entre les voies trophiques pélagique et benthique.

[Traduit par la Rédaction]

Introduction

Several recent studies using stable carbon isotopes ($\delta^{13}\text{C}$) have reported that benthic algal production appears to be an important contributor to the production of higher trophic levels in lakes (Hecky and Hesslein 1995; Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002). In parallel, it has been recognized that benthic primary pro-

duction can comprise a substantial portion of whole-lake primary production, with the actual contribution depending on factors such as substrate, lake area, morphometry, and trophic state (Vadeboncoeur et al. 2002, 2003). It is notable that benthic pathways appear to be important even in large lakes in which benthic primary production is expected to be a minor contributor at the whole-lake level (Bootsma et al. 1996). Based in part on this observation, Hecky and

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Hesslein (1995) suggested that benthic primary production is more efficiently transferred up the food chain and incorporated into consumer biomass relative to pelagic production. This would suggest that benthic trophic pathways are even more important than one would expect given their relative contributions to whole-lake primary production.

Though some limnological studies have recognized the potential for these dual trophic pathways in lakes (Lindeman 1942; Likens 1985; Jónasson et al. 1990), a pelagic-based paradigm has clearly dominated studies of lakes, particularly during recent decades. Viewing lakes as potentially composed of dual trophic pathways leads to consideration of how benthic and pelagic production and processes are linked (Schindler and Scheuerell 2002; Vadeboncoeur et al. 2002; Vanni 2002). If benthic pathways are as energetically important as indicated by stable isotope surveys, then it is imperative that their role in whole-lake production dynamics is understood. For example, studies that consider only pelagic production would tend to underestimate the productive capacity of ecosystems. Also, the assumption that phytoplankton production represents whole-lake production leads to an overestimate of the efficiency of energy transfer from primary producers to higher consumers if they exploit alternative (benthic and terrestrial) resources. Finally, a number of anthropogenic stresses on aquatic systems directly affect energy flow pathways. Exotic species such as zebra mussels (*Dreissena polymorpha*) and rusty crayfish (*Orconectes rusticus*) can reshuffle production pathways and affect energy flow and trophic efficiencies (Lodge et al. 1994; Karatayev et al. 2002). Lake eutrophication directly affects the distribution of primary and secondary production between habitats in lakes (Vadeboncoeur and Lodge 2000), and the removal of coarse woody habitat from lakes is correlated with reduced growth rates of recreationally important fish species (Schindler et al. 2000). Understanding the linkages between these dual trophic pathways is imperative in light of these management challenges.

Stable isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) are useful tracers of energy flow pathways and niche partitioning in aquatic food webs (Peterson and Fry 1987; Fry 1988; Kelly et al. 2004). For non-herbivores, there is a 3.4‰ ($\pm 0.4\%$) increase in $\delta^{15}\text{N}$ from prey to predator, such that $\delta^{15}\text{N}$ reflects a consumer's trophic position (Minagawa and Wada 1984; Hesslein et al. 1991; Vander Zanden and Rasmussen 2001). Stable carbon isotope values ($\delta^{13}\text{C}$) tend to be conserved between prey and predator. The $\delta^{13}\text{C}$ of phytoplankton is isotopically depleted relative to benthic algae (Hecky and Hesslein 1995; Vander Zanden and Rasmussen 1999) and can be used to estimate the contributions of littoral and pelagic production to higher trophic levels (Hecky and Hesslein 1995; Vander Zanden and Rasmussen 2001). Thus, concurrent examination of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ allows for descriptions of lake food webs in terms of energy sources and trophic position (Hecky and Hesslein 1995).

In this study, we quantify energy flow and ecological efficiencies for both benthic and pelagic food chains in a well-studied subalpine lake, Castle Lake, California. Our analysis is based on estimates of benthic and pelagic components of primary and secondary production, combined with gut content and stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) analysis of food web pathways (Grey et al. 2002). The simple food web structure

of Castle Lake provides an opportunity to track energy flow through benthic and pelagic pathways to higher trophic levels and to test the hypothesis that trophic energy transfer is more efficient along benthic pathways (Hecky and Hesslein 1995).

Materials and methods

Study site

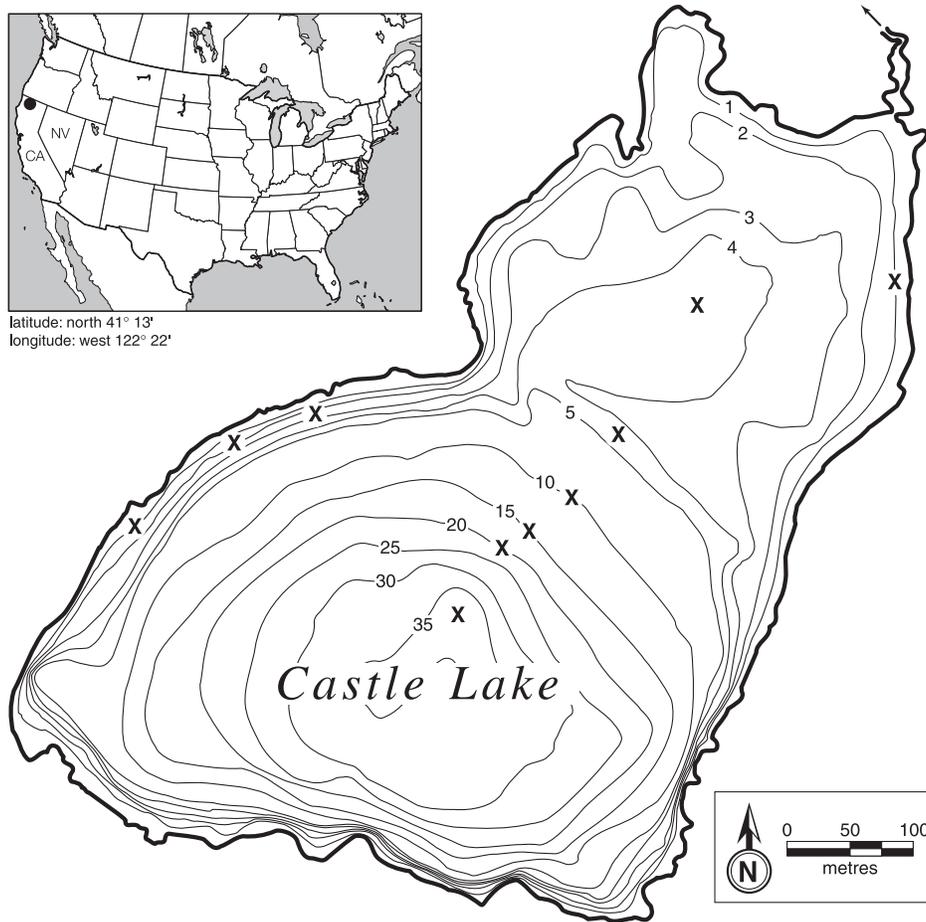
Castle Lake (Fig. 1) is located in a protected cirque basin in the Siskiyou Mountains of Northern California (41°13'N, 122°22'W, elevation = 1657 m). It has a maximum depth of 35 m, a mean depth of 11.4 m, summer epilimnion depth averaging 6 m, and a surface area of 20.1 ha. Castle Lake is typically ice-covered for >200 days per year (typically November to June), and mean summer Secchi depth ranges from 9 to 13 m (Elser et al. 1995). Water chemistry, Secchi depth, and phytoplankton production have been monitored annually since 1959 by researchers at University of California – Davis, and there have been no directional changes in water quality variables over this period (Jassby et al. 1990; Elser et al. 1995). Approximately 50% of the surface area of the lake overlies littoral habitat <6 m deep (Axler and Reuter 1996). This habitat is dominated by highly organic sediment (~90%) and rocks (~10%). Macrophytes are sparse and benthic primary production is dominated by periphyton. Castle Lake lacks zooplankton predators such as *Mysis* and *Chaoborus* but supports three fish species: annually stocked rainbow trout (*Oncorhynchus mykiss*) and self-sustaining populations of brook trout (*Salvelinus fontinalis*) and golden shiner (*Notemigonus crysoleucas*).

Pelagic primary production

We measured pelagic and benthic primary productivity along depth profiles and calculated whole-lake productivity using lake bathymetry (Fig. 1), incident solar radiation, and light attenuation rates. Phytoplankton primary productivity (PPR_p) and chlorophyll were measured weekly at the deepest part of the lake between late June and mid-August 2000. Water was collected at 13 depths between the surface and 30 m, and duplicate samples were incubated in situ at each depth using a standard ^{14}C pelagic primary production method, which is described elsewhere (Goldman et al. 1963; Goldman 1968). Total daily incident solar radiation was measured throughout the summer with a LI-COR Li-200 pyranometer. We took weekly light profiles on the days that photosynthesis was measured using a LI-COR Li-193 quantum spherical sensor. Daily phytoplankton productivity rates ($\text{mg C}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$) were calculated by dividing productivity measured during the incubation period by the fraction of total daily photosynthetically active radiation received during the incubation.

For each sample depth, we averaged daily phytoplankton productivity from all sample dates ($n = 7$) to produce a single average summer depth profile of PPR_p (Fig. 2a). Total areal phytoplankton production was estimated using the following equation:

Fig. 1. Bathymetric map of Castle Lake, California, USA. Zoobenthos sampling locations are indicated with an "X".



$$(1) \quad \text{TPPR}_p = \frac{\left(\sum_{z=0}^{30} V_z \text{PPR}_{p_{z+0.5}} \right)}{A_0}$$

where TPPR_p is total pelagic production per square metre of lake ($\text{g C} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$), z is depth, V_z is the volume of water between depth z and $z + 1$ (calculated as a frustum; Wetzel 2001), A_0 is lake surface area, and $\text{PPR}_{p_{z+0.5}}$ is the average summer phytoplankton productivity in the middle of each 1 m depth stratum calculated from the linear interpolation between depths of PPR_p (Fig. 2a).

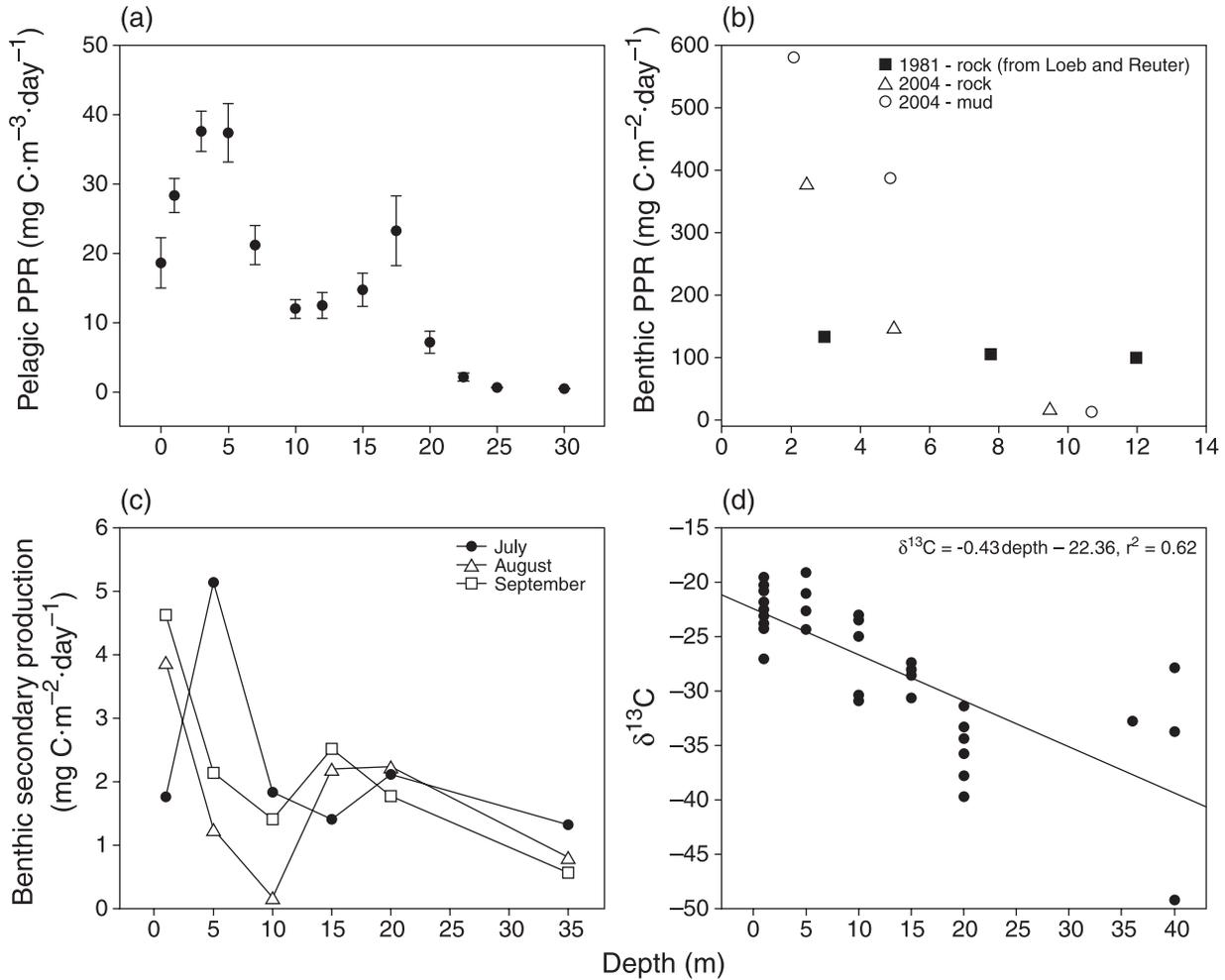
Benthic primary production

Bulk oxygen exchange methods were used to estimate benthic primary productivity on sediment (epipelic) and rock (epilithic) from three depths on one occasion during mid-August 2004. To measure epilithic primary productivity, we placed three light and two dark chambers over large boulders at each of three depths. Each chamber (inner dimensions 10 cm × 10 cm × 8 cm high) was sealed to the rock by placing a 2 kg ring of lead shot over a 10 cm neoprene skirt that extended from the bottom edge of the chamber. Water samples were withdrawn through a port sealed with a serum stopper, and a manually operated paddle was used to disrupt oxygen gradients immediately before withdrawing water samples. Water samples were removed with a 60 cm³ syringe at

the beginning of incubations and upon termination 2 h later. Water samples were fixed for Winkler titration immediately after divers returned to the surface. For epipelic primary productivity, we collected intact sediment cores (5 cm diameter × 8 cm deep, three light, two dark) in acrylic tubes at three depths and incubated them for 2 h at depth. Upon retrieving the cores, overlying water was removed and fixed for Winkler titrations. We calculated gross primary production per square metre of substratum as the net hourly oxygen increase in the light chambers plus the hourly community respiration rate in the dark chambers.

Our approach for extrapolating benthic productivity to the whole lake was slightly different than that for phytoplankton. Benthic productivity is strongly dependent on light (Vadeboncoeur et al. 2001), and our light data were more comprehensive than our benthic productivity data. Therefore, we used daily solar radiation data for the month of August to calculate whole-lake productivity based on our more limited (compared with phytoplankton) in situ production measurements. Benthic primary productivity (PPR_B) was measured during midday in full sun and thus represents $P_{B_{\max}}$ at the three depths for both sediment and rock (sediment, $P_{B_{\max}} = -6.55 \times \text{depth} + 76.4$, $r^2 = 0.98$; rock, $P_{B_{\max}} = -4.5 \times \text{depth} + 46$, $r^2 = 0.70$). $P_{B_{\max}}$ declined linearly with depth and reached zero at 11.7 m. Periphyton productivity was estimated daily at 0.1 m depth intervals from sunrise to sunset using the following equation:

Fig. 2. Depth-specific production values and carbon isotope values for Castle Lake, California: (a) mean summer phytoplankton primary production (PPR_P), (b) benthic primary production (PPR_B), (c) benthic secondary production (by month), and (d) δ¹³C of benthic chironomids and oligochaetes by depth.



$$(2a) \quad PPR_{B_z} = \Delta t \sum_{\text{sunrise}}^{\text{sunset}} P_{B_{\max z}} \tanh(I_{z_t}/I_k)$$

where $P_{B_{\max z}}$ at depth was estimated from the above regression equations. Surface irradiance was estimated at 0.5 h (Δt) time intervals using a sine function, and maximum light measured midday light intensities (McBride 1992). Light intensity at depth for each 0.5 h interval (I_{z_t}) was calculated from surface irradiance and K_d (0.24). The light intensity of onset of saturation (I_k) was set to 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Whole-lake benthic primary production ($\text{g C}\cdot\text{day}^{-1}$) was estimated at 0.1 m depth increments for depths between 1.5 and 12 m:

$$(2b) \quad TPRR_B = \frac{\left(\sum_{z=1.5}^{12} a_z PPR_{B_z} \right)}{A_0}$$

Periphyton mats were much less well developed between 0 and 1.5 m. To be conservative, we did not estimate primary production for these shallow depths. a_z is the surface area of sediments that occurs at a given water column depth and is calculated using the planar surface area of the lake at

the top and bottom of each depth interval ($a_z = A_z - A_{z+i}$, where i is the vertical depth increment (e.g., 0.1)). We made no correction for the increase in sediment surface area attributable to basin slope. Based on habitat surveys, we assumed that 10% and 90% of littoral surface area consisted of large rocks and soft sediments, respectively.

Macrophyte biomass and production are negligible in Castle Lake (Hagley 1989) and were thus ignored in our whole-ecosystem production calculations. Excluding macrophytes provided a more conservative measure of the contribution of benthic production to the lake.

Secondary production

Secondary productivity ($\text{mg C}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$) of the dominant zooplankton, *Daphnia rosea*, was estimated using the egg ratio method and data collected in 2000. This approach calculates the product of biomass and estimated growth rate for the summer growth season (Saunders and Lewis 1988). Numerical growth rate (b) is used as a proxy for biomass growth rate (Paterson et al. 1997). A Schindler trap (12 L volume, 80 μm mesh) was used to collect zooplankton four times (June, July, August, September) from depths of 1, 3, and 5 m (epilimnetic) during day (1300) and night (2200).

Using the equation of Paloheimo (1974), *Daphnia* production (volumetric) was estimated as the mean of the four nighttime epilimnetic samples. Biomass was converted to carbon by assuming 40% carbon content (dry weight). Whole-lake *Daphnia* production was estimated as the product of epilimnetic volume (depth of 6 m) and the volumetric estimate of *Daphnia* production from nighttime epilimnetic samples. The *Daphnia* production estimate was converted to whole-lake zooplankton production by multiplying by 1.24, which is the average weekly ratio of zooplankton production to *Daphnia* production estimated from 1996 data (S.-K. Park, unpublished data).

Benthic secondary production was estimated as the product of individual mass, population density, and estimated production to biomass (*P/B*) ratios (Strayer and Likens 1986). Zoobenthos samples were collected along a single depth transect at 1, 5, 10, 15, 20, and 35 m (Fig. 1) on 18–19 July, 22–25 August, and 12–13 September 2000. On soft substrates (>2 m depths), each sample was a composite of four Ekman grab samples (0.0225 m²). Four additional littoral zone samples were collected from hard or heterogeneous substrates (<2 m depths) on each date. A snorkeler used a battery-powered underwater suction sampling device similar to that described by Taylor et al. (1995) to collect organic material to a maximum depth of 10 cm within a randomly placed 0.25 m quadrat. The benthic samples were sieved (500 µm), sorted, and preserved in 70% ethanol. Invertebrates were identified to family (Chironomidae and Oligochaeta only) or most often genus, enumerated, dried at 70 °C for 24 h, and weighed. Taxon-specific annual *P/B* was estimated from the invertebrate allometric equation (Banse and Mosher 1980). *P/B* was multiplied by biomass (mg·m⁻²) at each site for each taxon (genus or family), giving the taxon-specific annual production (mg·m⁻²·year⁻¹). Summing these across taxa at a sampling site gave an estimate of total annual production (mg·m⁻²·year⁻¹) for a site. Annual production estimates were converted into daily carbon units (mg C·m⁻²·day⁻¹) by assuming that dry biomass was 45% carbon by weight (Strayer and Likens 1986; Wetzel 2001) and dividing annual production by 150, which is the number of ice-free days. By dividing by the number of ice-free days (rather than by 365 (the total number of days in the year)), we maintain consistency with our other production estimates, which are based on the summer ice-free season only. Furthermore, the growth rate of benthic invertebrates (and thus secondary production) is low at the cold temperatures associated with the winter ice-cover period (Wetzel 2001; O'Sullivan and Reynolds 2004).

Summer averages for benthic secondary production were calculated for 1, 5, 10, 15, 20, and 35 m. Linear interpolation was used to estimate production at 1 m intervals at depths <5 m and 5 m intervals at depths > 5 m. Whole-lake benthic secondary production was estimated as $\sum a_z \text{BSP}_z$, where a_z is the surface area of sediments at depth z , as described for periphyton, and BSP_z is secondary production rate (mg C·m⁻²·day⁻¹) at depth z .

Fish

For each of the three fish species in Castle Lake, reliance on benthic, pelagic, and terrestrial sources was estimated using diet data and stable isotopes (below). We did not attempt

to estimate ecological efficiencies for fish in this study, though to generalize fish species-specific trophic reliance to the whole-lake level, we needed some way to weight the contribution of the three fish species to whole-lake fish production. One approach would be to weight the three fish species equally, though they likely differ in their contribution to whole-lake fish production. We used previous quantitative fish survey data to estimate production for the three species and weighted the contribution of the fish species according to estimated production. Elser et al. (1995) estimated fish density and biomass during the period 1989–1991 in Castle Lake. We used only data from 1989, the first year of three in which rainbow trout were not stocked in Castle Lake. The fish community in 1989 was still dominated by rainbow trout and would be most similar to the present-day rainbow trout stocking regime (S. Baumgartner, California Fish and Game, 601 Locust Street, Redding, CA 96001, USA, personal communication). Annual production of rainbow trout, brook trout, and golden shiner were approximated as the product of biomass from 1989 hydroacoustic surveys (gill netting and purse seining used to partition according to species) and the annual *P/B* for each species reported by Randall and Minns (2000). Contributions of the three fish species to total fish production were estimated to be 42% brook trout, 45% rainbow trout, and 13% golden shiner. Isotope-based estimates of resource use for each fish species (mean from the two methods) were weighted according to the above estimates of fish species contribution to total fish production.

Stable isotopes

Benthic macroinvertebrates were collected for stable isotope analysis during the summer of 2000 at the same sites (Fig. 1) and dates as the estimates of benthic secondary production and were sorted to genus or family. Samples collected at 1 m depths were considered shallow water sites. Terrestrial invertebrates were collected from vegetation within 1 m of shore using a sweep net or were recovered from fish stomachs. Terrestrial invertebrate taxa were identified to family. Stable isotope analysis was performed on samples identified to genus or family, but values were later aggregated to family or order for reporting (Table 1; Fig. 3).

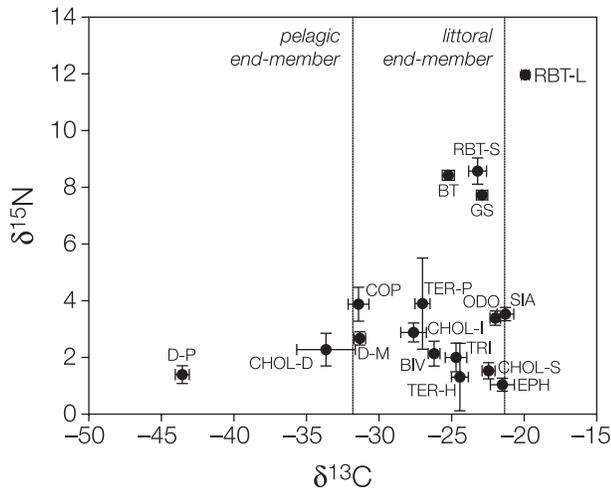
Zooplankton was collected for stable isotope analysis on eight dates between 28 June and 15 September during 1999 and 2000. Samples were collected by 30 m vertical tows using an 80 µm mesh zooplankton net near the deepwater sampling station. *Daphnia rosea*, *Diatomus novamexicanus*, and *Holopedium gibberum* were sorted and analyzed separately. On five dates, profundal *Daphnia middendorffiana* (profundal-dwelling *Daphnia*) were collected from 30 to 34 m using a Schindler trap (80 µm mesh).

Rainbow trout, brook trout, and golden shiner were collected using gill nets, minnow traps, and angling for stable isotope analysis and gut content enumeration from 27 June to 10 September 2000 (Table 2). Additionally, six large (>30 cm; mean length = 39 cm) rainbow trout were angled through the ice on 5 May 2001. Stomach contents were removed within 1 h of capture and immediately frozen. Contents were later identified to the lowest taxonomic level possible (typically family) and weighed. Contents were categorized as detritus, fish, zooplankton, terrestrial insects,

Table 1. Stable carbon and nitrogen isotope data (mean values and 1 standard error, SE) from Castle Lake biota collected in 2000.

Taxa	n	$\delta^{15}\text{N}$	SE	$\delta^{13}\text{C}$	SE	Depth or habitat
<i>Daphnia rosea</i>	11	2.7	0.2	-31.3	0.4	Epilimnion and metalimnion
<i>Diaptomus novamexicanus</i>	8	3.9	0.6	-31.4	0.7	Epilimnion and metalimnion
<i>Holopedium gibberum</i>	3	—	—	-33.5	1.3	Epilimnion and metalimnion
Oligochaeta–Chironomidae	19	1.5	0.3	-22.4	0.4	Littoral benthic
Ephemeroptera	15	1.0	0.2	-21.5	0.8	Littoral benthic
Odonata	18	3.4	0.2	-22.0	0.3	Littoral benthic
Megaloptera	8	3.5	0.2	-21.3	0.6	Littoral benthic
Trichoptera	15	2.0	0.5	-24.6	0.8	Littoral benthic
Bivalvia	4	2.1	0.4	-26.2	0.4	Littoral benthic
Terrestrial (predatory)	4	3.9	1.6	-27.0	0.5	Riparian
Terrestrial (herbivorous)	8	1.3	1.2	-24.4	0.6	Riparian
Oligochaete–Chironomidae	10	2.9	0.3	-27.6	0.9	Benthic (10–15 m)
Oligochaete–Chironomidae	12	2.3	0.6	-33.6	2.0	Benthic (20–40 m)
<i>Daphnia middendorffiana</i>	13	1.4	0.3	-43.5	0.5	Benthic–profundal (34 m)
California newt	2	6.4	0.5	-24.0	0.2	Littoral benthic
Brook trout	37	8.4	0.2	-25.2	0.4	—
Golden shiner	14	7.7	0.2	-22.9	0.4	—
Rainbow trout (<30 cm)	16	8.6	0.5	-23.2	0.7	—
Rainbow trout (>30 cm)	7	12.0	0.1	-19.9	0.2	—

Fig. 3. Stable isotope ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) food web diagram for the major taxa of Castle Lake, California. Symbols are as follows: D-P, profundal *Daphnia middendorffiana*; D-M, metalimnetic *Daphnia rosea*; COP, copepods; CHOL-D, deepwater chironomids and oligochates; CHOL-I, intermediate depth chironomids and oligochates; CHOL-S, shallow-water chironomids and oligochates; BIV, bivalves; TRI, trichoptera; EPH, ephemeroptera; ODO, odonates; SIA, sialids; TER-P, predatory terrestrial insects; TER-H, herbivorous terrestrial insects; GS, golden shiner (*Notemigonus crysoleucas*); BT, brook trout (*Salvelinus fontinalis*); RBT-S, small (<30 cm) rainbow trout (*Oncorhynchus mykiss*); RBT-L, large (>30 cm) rainbow trout.



aquatic insects, and unidentified insects. Not enough golden shiners were collected in 2000 for an adequate diet assessment. Detritus comprised <0.2% of gut content for both salmonids and was thus not included further in the analysis. Twenty-five percent of the total gut content (dry weight) for rainbow trout and 15% for brook trout could be classified no further than unidentified insects. This prey category was

omitted so that diets are expressed as percentage of identifiable prey items to total gut content weight (dry weight). The effect of this assumption is conservative in that it would tend to overestimate the importance of zooplankton to fish diets.

Dorsal muscle tissue was removed from each fish and frozen for stable isotope analysis. Fish and invertebrate samples were dried at 60 °C for at least 24 h and ground into a fine powder using mortar and pestle. Samples were packed into 8 mm × 5 mm tin capsules and analyzed for nitrogen and carbon isotope signatures using continuous flow isotope ratio mass spectrometry (20–20 mass spectrometer; Europa Scientific, Sandbach, UK). Isotopic ratios were expressed as a per mil (‰) deviation defined by the following equations: $\delta^{13}\text{C} = \{({}^{13}\text{C}/{}^{12}\text{C})_{\text{sample}} / [({}^{13}\text{C}/{}^{12}\text{C})_{\text{standard}} - 1]\} \times 1000$ and $\delta^{15}\text{N} = \{({}^{15}\text{N}/{}^{14}\text{N})_{\text{sample}} / [({}^{15}\text{N}/{}^{14}\text{N})_{\text{standard}} - 1]\} \times 1000$. More positive values are isotopically enriched, meaning that they contain proportionally higher concentrations of the heavier ^{13}C or ^{15}N isotope. Replicate samples and a standard material were analyzed approximately every 20 samples for quality control. Replicate variation was less than 3% and machine analytical error was within 0.2‰ for both $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$.

Isotope models

Zoobenthos, zooplankton, and terrestrial insects are all known prey of Castle Lake fishes. Each of these prey items have a unique $\delta^{13}\text{C}$ value, though they can not be differentiated using $\delta^{15}\text{N}$. Finding a unique solution for the contribution of these three sources would require two tracers. Here, we use two approaches to approximate contributions of these three sources to fish production. First, we apply the probabilistic mixing model (IsoSource, version 1.2) of Phillips and Gregg (2003), which calculates the range of possible solution values for the three potential sources. End-members for the mixing model were as follows: pelagic (mean $\delta^{13}\text{C}$ values of individual, nonprofundal zooplankton; $n = 22$, -31.6‰); terrestrial (mean of all terrestrial insects; $n = 12$, -25.3‰);

Table 2. Diet data, expressed as percentage of total gut volume or weight, from brook trout (*Salvelinus fontinalis*), rainbow trout (*Oncorhynchus mykiss*), and golden shiner (*Notemigonus crysoleucas*) from Castle Lake from multiple time periods.

Year	<i>n</i>	Planktonic	Benthic	Terrestrial	Fish	Reference
Brook trout						
1941–1944	180	22	28	48	3	Wales 1946
1963–1965	175	14	76	10	0	Swift 1970
1989	— ^a	18	74	8	0	Elser et al. 1995
1990	— ^a	18	53	29	0	Elser et al. 1995
1991	— ^a	0	26	74	0	Elser et al. 1995
2000	43	<0.5	91	6	2	This study
Mean		12	58	29	1	
SD		9.5	26.9	27.3	1.3	
Rainbow trout						
1941–1944	134	13	19	62	7	Wales 1946
1963–1965	275	33	22	45	0	Swift 1970
1989	— ^a	24	44	33	0	Elser et al. 1995
1990	— ^a	20	66	15	0	Elser et al. 1995
1991	— ^a	0	36	64	0	Elser et al. 1995
2000	24	0	59	41	0	This study
Mean		11	51	38	0	
SD		12.6	13.4	20.4	—	
Golden shiner						
1989	— ^a	40	20	40	0	Elser et al. 1995
1990	— ^a	50	4	46	0	Elser et al. 1995
1991	— ^a	47	25	28	0	Elser et al. 1995
Mean		46	16	38	0	
SD		5.1	11.0	9.2	—	

^aElser et al. (1995) reported that diets were analyzed for “up to 50 individuals of each species” in each year.

and littoral (mean of Ephemeroptera, Oligochaeta, and Chironomidae from <5 m depth; *n* = 34, −22.0‰). These particular primary consumer taxa were chosen as the littoral end-member because they are ¹³C-enriched and are thus most indicative of a pure periphyton signal.

To provide an independent estimate of benthic reliance and to validate results from the Phillips and Gregg (2003) approach, we use gut content data on percent consumption of terrestrial prey to constrain the mixing model so as to provide a unique solution for zoobenthos and zooplankton sources. Assuming no fractionation, the δ¹³C of a consumer (fish) is the diet-weighted average of its various prey:

$$(3) \quad \delta^{13}\text{C}_{\text{cons}} = (\delta^{13}\text{C}_{\text{terr}} t) + (\delta^{13}\text{C}_{\text{ben}} b) + (\delta^{13}\text{C}_{\text{pel}} p)$$

where *t*, *b*, and *p* are the proportional contributions of terrestrial, benthic, and pelagic prey, respectively. By approximating the percent contribution of terrestrial insects from gut content data from Castle Lake (Wales 1946; Swift 1970; Elser et al. 1995), there exists a unique solution for the mixing model. From eq. 3, setting *p* = 1 − (*b* + *t*) and solving for *b* yields

$$(4) \quad b = -\frac{(\delta^{13}\text{C}_{\text{terr}} t) + \delta^{13}\text{C}_{\text{pel}} - (\delta^{13}\text{C}_{\text{pel}} t) - \delta^{13}\text{C}_{\text{cons}}}{\delta^{13}\text{C}_{\text{ben}} - \delta^{13}\text{C}_{\text{pel}}}$$

Contributions of pelagic and benthic prey to fish diets were estimated using eq. 4 and the mean terrestrial consumption values from Table 2. We increased and decreased (relative to

the mean value) the values for percent terrestrial diet by 30% (relative to the original value) to assess sensitivity to this assumption.

Ecological efficiencies and benthic–pelagic coupling

Ecological efficiencies (EE_{*i*}) were calculated separately for benthic and pelagic pathways:

$$(5) \quad \text{EE}_i = \left(\frac{P_{n,i}}{P_{n-1,i}} \right) \times 100$$

where EE_{*i*} is the ecological efficiency for pathway *i*, *P*_{*n,i*} is the production at trophic level *n* supported by pathway *i*, and *P*_{*n-1,i*} is the production at trophic level *n* − 1 from pathway *i*.

Benthic secondary production is supported by a mix of pelagic (phytoplankton fallout) and benthic–littoral primary production sources. To estimate the relative contribution of these two primary production sources to zoobenthos, we estimated zoobenthos δ¹³C at each of 12 depth intervals from the regression equation in Fig. 2*d*. For each depth, we used a two-source mixing model (pelagic end-member = −31.6‰, littoral end-member = −22‰) to estimate the contribution of pelagic (phytoplankton) primary production. The contribution (%) of pelagic sources to benthic secondary production at the whole-lake level was estimated as follows:

$$(6) \quad \text{ZP}_{\text{pel}} = \sum a_z \text{BSP}_z \text{pel}_z$$

where a_z is lake area (m^2) at depth z , BSP_z is benthic secondary production rate ($\text{mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) at depth z , and pel_z is percent pelagic reliance (from mixing model above) at depth z . Dividing this value by total benthic secondary production yields the (proportional) contribution of pelagic primary production to benthic secondary production.

Results

Primary and secondary production

The daily summer average phytoplankton primary production (PPR_p; $\text{mg C}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$) varied as a function of lake depth, with peak values of $37 \text{ mg C}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$ at 3–5 m and a secondary peak of $23 \text{ mg C}\cdot\text{m}^{-3}\cdot\text{day}^{-1}$ at 17.5 m (Fig. 2a). Benthic primary production declined with depth and was effectively 0 at 12 m for both epilithic and epipellic primary production (Fig. 2b). The mean coefficient of variation for benthic primary production measurements at a site was 31%. Benthic primary production values from 2004 were higher than those reported by Loeb and Reuter (1981). Whole-lake primary production (benthic + pelagic) was estimated to be $464 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ (total production = $93\,300 \text{ g C}\cdot\text{day}^{-1}$). Of this, 47% was benthic ($220 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$) and 53% was pelagic ($244 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$).

Benthic secondary production for Castle Lake was estimated to be $2.4 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. Benthic secondary production tended to decrease with depth ($\text{BSP} = -0.061 \times \text{depth} + 2.94$, $r^2 = 0.28$; Fig. 2c). Benthic secondary production estimates show a secondary peak at intermediate depths (15–20 m). Chironomid and oligochaete carbon isotope values become isotopically depleted with depth (Fig. 2d), indicating a shift from benthic algae to phytoplankton-derived detritus with depth. Zooplankton production was estimated to be $5.5 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$. Whole-lake secondary production was thus estimated to be $7.9 \text{ mg C}\cdot\text{m}^{-2}\cdot\text{day}^{-1}$ ($1583 \text{ g C}\cdot\text{day}^{-1}$), with approximately 30% being benthic ($475 \text{ g C}\cdot\text{day}^{-1}$) and the remaining 70% ($1108 \text{ g C}\cdot\text{day}^{-1}$) being pelagic.

Stable isotopes and diets

Mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (± 1 standard error, SE) for major taxonomic groups of the Castle Lake food web were calculated (Table 1), and values were plotted in a $\delta^{13}\text{C}$ – $\delta^{15}\text{N}$ biplot (Fig. 3). Zooplankton $\delta^{13}\text{C}$ values averaged -31‰ , whereas littoral benthic invertebrates were in the -21‰ to -25‰ range. Terrestrial insects averaged -25‰ . Profundal zoobenthos (chironomids and oligochaetes) and profundal-dwelling *Daphnia middendorffiana* exhibited $\delta^{13}\text{C}$ values that were highly depleted (Table 1).

Rainbow trout (<30 cm), brook trout, and golden shiner all had $\delta^{15}\text{N}$ values $\sim 4\text{‰}$ above that of invertebrates and $\delta^{13}\text{C}$ values indicative of benthic- and (or) terrestrial-dominated diets. Rainbow trout $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ increased with size, with large (>30 cm) rainbow trout exhibiting elevated nitrogen and carbon signatures, indicating a diet of small benthivorous fishes.

In 2000, brook trout gut contents were dominated by zoobenthos (90%), with minor contributions of terrestrial insects (Table 2). Rainbow trout smaller than 30 cm consumed a mix of zoobenthos and terrestrial insects. Large (>30 cm) rainbow trout ($n = 7$) all had empty stomachs. Neither rainbow trout nor brook trout consumed substantial amounts of

zooplankton in 2000. Historical data also showed that brook trout and rainbow trout preyed primarily on zoobenthos (averaging 50%–60%) and terrestrial insects (averaging 30%–40%) (Wales 1946; Swift 1970; Elser et al. 1995). Elser et al. (1995) reported that zooplankton were also a component (10%) of trout diets. We did not conduct gut content analysis for golden shiners, but historical data (1989–1991) indicate that golden shiners consumed a mix of zooplankton (46%), terrestrial insects (38%), and zoobenthos (16%). Fish diets varied widely from year to year and among studies (Table 2).

Stable isotopes also indicated high reliance of Castle Lake fishes on benthic prey. Mean (± 1 SD) zoobenthivory estimates using IsoSource 1.2 (Phillips and Gregg 2003) were 38% ($\pm 18\%$) for brook trout, 74% ($\pm 11\%$) for golden shiner, and 69% ($\pm 12\%$) for small rainbow trout (Table 3). Estimates based on eq. 4 (using gut content based estimates of terrestrial insect contributions to diet) were similar to those using IsoSource (Table 3). Increasing and decreasing estimates of terrestrial consumption by 30% produced a range of benthic reliance estimates (shown in parentheses in Table 3). Overall, isotope-based estimates of benthic reliance corresponded with dietary estimates, although stable isotopes indicated lower pelagic reliance than diet data for golden shiner.

Ecological efficiencies

Ecological efficiencies (primary production / secondary production) for benthic and pelagic pathways were estimated to be 1% and 3%, respectively (Fig. 4). Approximately 35% of whole-lake zoobenthic production in Castle Lake was supported by phytoplankton detritus. Adjusting for this reduced the ecological efficiency for the benthic primary–secondary production link from 1% to $\sim 0.6\%$.

The contributions of benthic, pelagic, and terrestrial prey in supporting Castle Lake fish were estimated to be 63%, 13%, and 24%, respectively. We did not estimate absolute ecological efficiencies at the invertebrate–fish link for benthic and pelagic pathways, because the available fish production data were from a different year than that of our study. We can estimate relative differences in benthic and pelagic ecological efficiencies and find that benthic ecological efficiency at the invertebrate–fish level is nearly 20 times higher than that for pelagic pathways (Fig. 4).

Discussion

Energy efficiencies

Benthic and, secondarily, terrestrial production pathways appear to be most important in supporting fish populations in Castle Lake, California. Although the pelagic zone supported the majority ($\sim 70\%$) of whole-lake secondary production, zooplankton production did not contribute substantially to the adult fish population. Rather, the primary energy source supporting fish was benthic, based on independent stable isotope and dietary evidence. This general result supports the hypothesis of Hecky and Hesslein (1995) that benthic production is efficiently passed up the food chain to higher consumers relative to pelagic primary production, though we also found that at the primary–secondary produc-

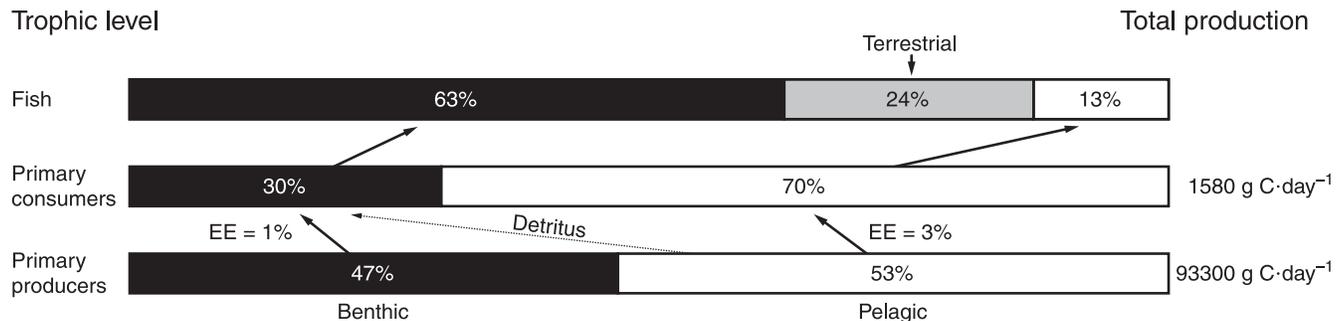
Table 3. Estimates (%) of the contributions of zooplankton, zoobenthos, and terrestrial prey to rainbow trout (*Oncorhynchus mykiss*), brook trout (*Salvelinus fontinalis*), and golden shiner (*Notemigonus crysoleucas*) in Castle Lake, California.

	$\delta^{13}\text{C}$ (‰)	Zooplankton (-31.6‰) ^a	Zoobenthos (-22‰) ^a	Terrestrial (-25.3‰) ^a
IsoSource (version 1.2)				
Rainbow trout (<30 cm)	-23.18	7.5 (5.5)	69.9 (13.9)	22.7 (16.1)
Brook trout	-25.2	18.4 (10.3)	37.0 (18.9)	44.6 (26.5)
Golden shiner	-22.86	6.3 (4.8)	74.4 (12.3)	19.3 (14.0)
Equation 4				
Rainbow trout (<30 cm)	-23.18	0	62 (56–70)	38
Brook trout	-25.2	23	47 (42–54)	29
Golden shiner	-22.86	0	62 (51–73)	38

Note: IsoSource (version 1.2) is from the method of Phillips and Gregg (2003). Values are mean (± 1 standard deviation). Equation 4 uses gut content data to approximate consumption of terrestrial prey. Values in parentheses are zoobenthivory estimates resulting from a 30% increase and 30% decrease, respectively, in terrestrial prey consumption.

^aValues in parentheses (after zooplankton, zoobenthos, and terrestrial) are end-member values used in mixing models.

Fig. 4. Contributions of benthic, pelagic, and terrestrial production to total production for primary producers, primary consumers, and fish in Castle Lake, California. Ecological efficiency = (predator production / prey production) \times 100.



tion link, pelagic trophic transfer appeared to be more efficient than the benthic pathway.

The stable isotope approach traces the ultimate source of primary production, such that profundal zoobenthos supported by phytoplankton detritus are considered to be pelagic in origin. We estimated that roughly 35% of whole-lake zoobenthos production in Castle Lake was supported by pelagic phytoplankton detritus. This has the effect of reducing the benthic primary–secondary ecological efficiency estimate, as profundal zoobenthos production is partially supported by pelagic resources. Fish stable carbon isotope values tend to be enriched, indicating little reliance on profundal resources. The approach of lumping littoral and profundal benthic prey as zoobenthos may not be appropriate, as fish seem to exploit the littoral component of the zoobenthos pool. The above discussion highlights the importance of considering benthic–pelagic coupling in its many forms, including the role of phytoplankton detritus in supporting profundal zoobenthos, and also highlights how zoobenthos from different habitats are used by higher trophic levels.

Our whole-lake estimates of benthic primary production in Castle Lake are higher than previous estimates of epilithic primary production for this lake (Loeb and Reuter 1981). This may be partly due to the differences in methods. In both Lake Tahoe and Castle Lake, our estimates of primary production on rocks using oxygen methods in 2004 were two to three times those using ^{14}C in the late 1970s (Loeb and Reuter 1981). However, given that we do not correct for

increased surface area due to littoral slope, the average hourly estimates of littoral primary production on rocks used here may not be substantially different than earlier measurements (Loeb et al. 1983). Additionally, we measured primary production on organic sediments, the dominant substratum in Castle Lake. Sediments consistently have five to 10 times higher rates of production than periphyton on rocks (Vadeboncoeur et al. 2001). The high metabolic activity of sediments relative to rocks in Castle Lake was also seen in a whole-lake epilimnetic nitrogen addition in which algae on sediments took up over 50% of added nitrogen (Axler and Reuter 1996). Indeed, previous estimates of whole-lake epipelagic production using ^{14}C indicated that whole-lake epipelagic primary production equaled or exceeded whole-lake phytoplankton production (Sanders 1976; Axler and Reuter 1996). Our measurements over 30 years later yielded the same result. Thus, we conclude that the difference in substratum, not the difference in methods, is primarily responsible for the higher rates of benthic primary productivity measured in this study.

Ecological efficiencies at the primary producer – primary consumer link differed between benthic and pelagic habitats. The ecological efficiency of the benthic primary producer – zoobenthos (0.5%–1%) link is lower than that for phytoplankton–zooplankton (3%). A part of this disparity could be attributed to using O_2 exchange methods for benthic algae and ^{14}C methods for phytoplankton. However, similar differences at the primary producer – primary consumer link have been observed in other lakes. In Lake Thing-

vallavatn, Iceland, the ecological efficiency between phytoplankton and zooplankton is 5.2%, whereas it is 2.1% between periphyton and zoobenthos (Jónsson 1992). The differences in ecological efficiency may be indicative of real, but as yet unexplored, ecological contrasts between habitats. Zooplankton can be efficient at depleting their food supply (Cyr and Pace 1993), but similar analyses are not available for epipelagic and benthic grazers. Furthermore, we included benthic predators (megalopterans and odonates) in our estimates of zoobenthic production, which has the effect of depressing estimates of ecological efficiency.

Our estimates of ecological efficiency (consumer production / prey production) are the result of two separate efficiencies: growth conversion efficiency (growth / consumption rate) and consumption efficiency (consumption rate / available production) (see Strayer 1991). The low ecological efficiencies reported here suggest that consumers are not efficiently consuming the available production at the preceding trophic level. Zooplankton appear to be an underexploited prey item of fish in this lake, though consumption by juvenile and young-of-the-year fishes was not quantified in this study. Previous studies indicate that this can be an important source of zooplanktivory in lakes (Post et al. 1997).

Why might ecological efficiencies be higher at the zoobenthos–fish link compared with the zooplankton–fish link? Clearly the specific feeding adaptations of the fish species being studied will influence relative prey profitability (Werner and Gilliam 1984). All three fish species in Castle Lake are known to have diverse diets, feeding on a mix of zoobenthos, zooplankton, surface insects, and fish as available (Wales 1946; Swift 1970; Elser et al. 1995), and none of these species is considered strict zooplanktivore or zoobenthivore.

One potential explanation for the efficient use of zoobenthic resources involves the differences in body size between zoobenthos and zooplankton. In Castle Lake, zoobenthos prey weights were, on average, more than two orders of magnitude larger than zooplankton weights. Furthermore, the zoobenthos size-frequency distribution has an extended tail of large-sized individuals. Even if our sampling protocol missed the small end of the zoobenthos size distribution, the existence of large-sized zoobenthic prey (relative to zooplankton) translates into greater foraging profitability for fish feeding on zoobenthos relative to zooplankton, though prey abundance and (or) availability undoubtedly also plays a role in determining relative prey profitability. The energetic benefits of feeding on benthic prey have been quantified in studies of optimal foraging theory in littoral fishes (Werner and Hall 1974), but the ecosystem-level implications for patterns of energy flow through linked food webs remain poorly appreciated.

In addition to these differences in prey body size, physical differences between pelagic and benthic habitats may influence the efficiency with which fish predators are able to exploit invertebrate prey. In the benthic environment, prey inhabit an environment that more closely resembles a two-dimensional surface. The result is that benthic secondary production is more spatially concentrated and potentially more easily detected and exploited by fish. In lakes with abundant macrophyte cover, the two-dimensional compari-

son may be less applicable, though prey resources are still likely to be spatially concentrated. The three-dimensional nature of the pelagic environment has the effect of diluting the zooplankton production base, particularly in deep lakes such as Castle Lake. This may challenge the food-gathering capacity of fishes, particularly those lacking specific adaptations for zooplanktivory. In addition to these physical habitat differences, both zoobenthos and zooplankton have evolved refuges from predation. Zooplankton may undertake daily vertical migrations to minimize predation risks from fish. Although zoobenthos are more concentrated in their two-dimensional habitat, the benthic substrate may offer zoobenthos a refuge from fish predation. It is likely that differences in both habitat structure and prey body size are responsible for the differences between benthic and pelagic ecological efficiencies.

Finally, differences in food quality between zoobenthos and zooplankton could also explain these efficiency patterns, though caloric content of zoobenthos was not notably higher than that of zooplankton (Cummins and Wuycheck 1971). Fatty acid biomarkers may be useful indicators of food quality for comparing benthic and pelagic trophic pathways (Muller-Navarra et al. 2000; Park et al. 2002).

Trophic dynamics

An earlier study in Castle Lake found that cessation of rainbow trout stocking resulted in a compensatory increase in golden shiner and brook trout recruitment and population size (Elser et al. 1995). The consequence was that total zooplanktivory actually increased as rainbow trout populations declined over the study period, and a corresponding, predation-driven shift in the zooplankton community was observed. In that earlier study, zooplankton constituted a portion of the diet of all three fish species. In the present study, zooplankton was found to be a minor prey item, which is consistent with our stable isotope results. Why the importance of zooplankton in fish diets differs between these time periods is not known, although fish diets can show a high degree of interannual variability.

Although consumption of benthic prey by fish is thought to subsidize top-down control in the pelagic zone in some systems (Schindler et al. 1996; Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002), this was not apparent in Castle Lake. Both stable isotopes and diet data indicate that zooplankton were a minor energy source for adult fish in 2000, and fish do not show a preference for foraging on zooplankton in this system. The low estimates of ecological efficiency for the pelagic trophic chain indicates that a small proportion of zooplankton production is consumed by adult fish, though as noted above, consumption by young-of-the-year fishes was not included in the analysis. The apparent low level of zooplanktivory has obvious implications for patterns of top-down control in the pelagic zone of Castle Lake. Strong (1992) defined trophic cascades as “runaway consumption”, that is, top-down control requires that predators efficiently exploit their prey (i.e., consume the available production). Our results strongly suggest that the zooplankton community was not regulated by top-down factors in 2000, though it should be noted that zooplankton averaged 12% of salmonid diets across all years for which data

were available, and golden shiner diets were nearly half zooplankton in the 1989–1991 period (Elser et al. 1995).

Rainbow trout are stocked into Castle Lake on an annual basis. In the years before our data collection (1997–1999), both catchable size fish (200–400 g) and fingerlings (2–4 g) were stocked at an average rate of 790 (range 500–1125) and 16 800 (15 000 – 20 000) fish per year, respectively. This species was supported primarily by terrestrial and benthic invertebrate prey, although $\delta^{15}\text{N}$ signatures indicate that large (>30 cm) rainbow trout are piscivorous, presumably feeding on juvenile brook trout and golden shiner, which appear to be supported by littoral production (based on high rainbow trout $\delta^{13}\text{C}$ values). Continued stocking of rainbow trout maintains the population, with a portion becoming large enough to become piscivorous. The consequence may be maintenance of intense predation on juvenile brook trout and golden shiners. Consistent with this suggestion, Elser et al. (1995) reported that stocking of rainbow trout suppressed natural recruitment of brook trout and golden shiner and that relaxing stocking during the period 1998–1991 allowed a recruitment boom for these two species.

Isotopic interpretations

As mentioned above, a mix of catchable size and juvenile rainbow trout are annually stocked into Castle Lake. Interpretation of isotopic signatures of this species could be confounded by the residual isotopic signature of their hatchery food, though this prospect seems unlikely. The hatchery-derived isotopic signature of stocked fingerlings would be rapidly diluted by fish growth in the Castle Lake environment (Fry and Arnold 1982; Hesslein et al. 1993). The hatchery isotopic signal of catchable size rainbow trout could be retained in the population for a period of many months. The small rainbow trout sampled were less than 200 g in weight, indicating they were stocked as fingerlings. The large rainbow trout captured in May 2001 ranged from 400 to 1190 g (mean = 760 g). If these fish had been stocked as catchable size fish, they would have spent at least a year in the lake, which would have allowed time for growth and tissue turnover to dilute the hatchery isotopic signal (Hesslein et al. 1991).

For Castle Lake fish, there were three main prey types, though they differed only in $\delta^{13}\text{C}$ values. IsoSource (version 1.2; Phillips and Gregg 2003) was used to estimate the mean and range of values for reliance on these three prey. As an alternative approach, we used an equation that provides a unique solution for a one-isotope mixing model with three sources, provided that the contribution of one source is known. Assumptions of this approach are that the contribution for the one source is correct and that prey contribution to diet is equivalent to assimilation. A benefit of using stable isotopes over direct diet data is that it offers a time-integrated measure of energy pathways and prey assimilation, whereas diet studies offer just a snapshot of which prey were consumed. This benefit is lost when we assume these two to be equivalent. Furthermore, error in the contribution of the known prey item to the consumer diet produces error in the two sources being estimated. Here, we note a high degree of diet variation among years, such that a major source of error could be introduced in this term. Nevertheless, we found that the mean prey reliance (percentage of diet) given

by IsoSource (version 1.2) and estimates from eq. 4 corresponded quite well (eq. 4 estimate = $0.791 \times \text{IsoSource} + 6.86$, $n = 9$, $r^2 = 0.75$).

The extreme negative $\delta^{13}\text{C}$ signatures of profundal primary consumers in Castle Lake (-44‰) are some of the more negative isotopic values published. One explanation is the uptake of isotopically light, respired carbon by phytoplankton (Rau 1978, 1980; Peterson and Fry 1987), although if this were the case, this depleted carbon signature would also be detected in metalimnetic zooplankton. Another explanation is the effect of methanogenic bacteria (Fry and Sherr 1984). Methanogenesis occurs in anoxic hypolimnetic sediments, producing ^{13}C -depleted CH_4 (-50‰) and bacteria (-64‰) (Whiticar et al. 1986; Jones and Grey 2004). It is evident from fish $\delta^{13}\text{C}$ values in Castle Lake that these ^{13}C -depleted profundal primary consumers are not an energy source to higher consumers.

Sources of error

There are a number of potential sources of error associated with our assessment of benthic and pelagic productivity and ecological efficiencies for Castle Lake. Central to our approach is the assumption that a relatively small number of productivity estimates can be extrapolated to make broad generalizations about whole-lake productivity and trophic pathways in Castle Lake. Benthic primary productivity was estimated on a single date at three depths and two habitats, and light data were used to generalize these measurements to the ice-free season. Similarly, pelagic primary production was based on seven primary production vertical profiles from 2000 and was taken as representative of Castle Lake. *P/B* ratios were used for estimating benthic secondary production from biomass data, an approach that can be subject to error because *P/B* is not likely a constant for a taxa or species of a given body size. For zooplankton, we used the egg ratio method to estimate production for the dominant zooplankton, *Daphnia rosea*. We extrapolated this estimate to the zooplankton community using data on the contribution of *Daphnia* to community zooplankton production. Though *Daphnia* are the dominant zooplankton in Castle Lake, interannual differences in zooplankton communities would be another source of error in our production estimates. Clearly there are numerous sources of error involved in assessing benthic and pelagic trophic pathways, and our production estimates are undoubtedly important potential sources of error in this study. An additional limitation of this study was that we were not able to estimate fish production for Castle Lake, and we felt it was not justified to use fish data collected a decade earlier (Elser et al. 1995), as fish populations are likely to change over time. Fish production estimates using data from Elser et al. (1995) were only used to estimate relative contributions of the three fish species to fish production in Castle Lake.

Despite the above sources of error in our study, this analysis provides a broad-scale picture of energy flow and ecological efficiencies in a subalpine lake and highlights the importance of benthic trophic pathways at the whole-ecosystem level. It is critical to be aware of the potential sources of error and variability in the present analysis. We believe that it is equally important to expand this type of

analysis to a broader range of lakes using more refined methods and a more explicit assessment of fish production.

Recent stable isotope studies have revealed an important role for benthic energy flow pathways to higher trophic levels in lakes (Hecky and Hesslein 1995; Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002). These analyses have not been extended to combine stable isotope analysis of food web pathways with estimations of production at different trophic levels for benthic and pelagic food chains. The present paper presents such an analysis for Castle Lake, California, thus allowing simultaneous estimation of ecological efficiency along benthic and pelagic trophic pathways. Although primary production was nearly evenly split between the two habitats, invertebrate secondary production was dominated by pelagic production (70% of whole-lake secondary production). Despite this, fish were predominantly supported by benthic pathways, though an important limitation of our study was that we did not have a reliable estimate of fish production for Castle Lake. Still, our findings indicate an important role for benthic production in supporting higher trophic levels in this subalpine lake (Hecky and Hesslein 1995). Such patterns need to be examined in other systems, though this work indicates an important role of benthic pathways to higher trophic levels, likely as a result of the efficient exploitation of zoobenthos by fishes. This work builds on a long history of the study of energy flow pathways in lakes that dates back to Lindeman (1942) and highlights the value of integrated studies of benthic and pelagic processes in lakes (Vadeboncoeur et al. 2002). The view that benthic and pelagic food chains can be treated as separate entities is not supported by a growing body of literature revealing the importance of habitat coupling in lakes (Vanni 1996; Schindler and Scheuerell 2002; Vander Zanden and Vadeboncoeur 2002).

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