

## Nutritional quality of food resources for zooplankton (*Daphnia*) in a tidal freshwater system (Sacramento–San Joaquin River Delta)

Anke B. Müller-Solger,<sup>1</sup> Alan D. Jassby, and Dörthe C. Müller-Navarra

Department of Environmental Science and Policy, University of California—Davis, California 95616

### Abstract

We examined the relative nutritional values of natural phytoplankton and particulate detritus for zooplankton growth in a detritus-rich environment. Seston was collected seasonally from four different habitat types in a tidal freshwater system and fed to juvenile *Daphnia magna* under controlled culture conditions by use of a flow-through design. Seston particulate organic carbon (POC) and chlorophyll *a* contents ranged from ~330 to 3,800  $\mu\text{g L}^{-1}$  POC and 1.4 to 45  $\mu\text{g L}^{-1}$  Chl *a*. A partial residual analysis revealed that detrital carbon concentrations were only weakly related to *Daphnia* growth, whereas Chl *a* proved to be highly predictive of *Daphnia* growth rates across all investigated habitat types. Overall, habitat type had a strong effect on growth rates, whereas season of seston collection did not, but differences among habitats could be attributed to differing Chl *a* concentrations. The results from this study imply that, even in systems with overwhelming amounts of detrital carbon from a variety of sources, nutritional factors associated with phytoplankton can be dominant in regulating zooplankton growth.

Detritus usually constitutes the majority of particulate organic matter (POM) suspended in downstream reaches of rivers, small water bodies, and oceans (Melack 1985). Detritus thus represents a substantial pool of potentially usable energy and carbon for primary consumers such as zooplankton, and there is evidence that zooplankton can ingest and assimilate considerable amounts of detrital carbon of aquatic (Mann 1988) and terrestrial (Hessen et al. 1990) origin. However, there are relatively few published studies on the actual nutritional value of detritus for zooplankton. Several investigators have fed artificially produced detritus derived from various source materials such as algae, macrophytes, and terrestrial plants to zooplankton (e.g., Wehr et al. 1998). Results from these studies showed that detritus derived from algae and aquatic vascular plants is generally more efficiently assimilated by zooplankton than detritus derived from terrestrial plants. The artificially produced detritus was usually less nutritious than living algae, except when the phytoplankton community was dominated by cyanobacteria of particularly poor nutritional quality (Repka 1998). In natural systems, the importance of algae for primary consumer nutrition is supported by the results of studies that have used

nutritional tracers such as lipid biomarker compounds and carbon isotopes (e.g., Canuel et al. 1995; Finlay 2001).

Although feeding studies with different types of food as well as tracer studies can identify important food sources for consumers, they cannot identify which substances contained in unaltered POM of naturally diverse origins actually regulate consumer growth in natural systems. Such substances may be elements or essential biochemical compounds that are not sufficiently supplied by the quantitatively dominant food source. Growth bioassays with seston-containing natural POM as a food source and simultaneous analysis of seston constituents can provide information on substances potentially limiting consumer growth in nature. Such growth bioassays have led to the identification of certain essential fatty acids and mineral nutrients as factors that potentially limit zooplankton growth in natural environments (Müller-Navarra et al. 2000; Elser et al. 2001). These types of studies are still rare, however, and even fewer studies have been conducted in systems with substantial amounts of detrital carbon such as estuaries and small lakes (Ojala et al. 1995; Burdloff et al. 2000).

POM in developed estuaries contains carbon from many potential sources of varying quality such as phytoplankton, terrigenous organic matter (including agricultural run-off), emergent and submerged aquatic vascular plants, and sewage effluent. Although the carbon sources in many streams and estuaries have been quantified through carbon budgets and loading models (Webster and Meyer 1997; Howarth et al. 2000), much remains to be learned about the nutritional value of the identified carbon sources. This information is imperative to construct functionally accurate food web models for scientific as well as resource management purposes.

The goal of our study was to evaluate the relative nutritional values of algal and detrital carbon for the growth of suspension feeding zooplankton across several habitat types of a tidal freshwater system. In this investigation, we use the term “detritus” in its traditional definition by Odum and de la Cruz (1963) as dead POM with associated microorganisms. Dissolved organic carbon, which has been included in

<sup>1</sup> To whom correspondence should be addressed (amueller@water.ca.gov).

### Acknowledgments

We thank J. Cloern, W. Sobczak, and the CALFED POM team as well as C. R. Goldman and the University of California—Davis limnology group for invaluable assistance at all stages of this project. We also thank K. Forshay, A. Liston, and S.-F. Kuok for their dedicated assistance in field and laboratory and Cosumnes and Yolo Bypass researchers for help with sample collection and for fruitful discussions. This work was funded by the CALFED program (1425-98-AA-20-16240). A.D.J. is also grateful for support from the U.S. Environmental Protection Agency (R819658) through the Center for Ecological Health Research at the University of California—Davis. Although the U.S. EPA partially funded preparation of this document, it does not necessarily reflect the views of the agency and no official endorsement should be inferred.

more recent definitions of detritus (Wetzel et al. 1972), is not part of this study.

We conducted a series of standardized laboratory growth assays in which we fed natural seston collected during different seasons and from several habitats to a laboratory strain of the suspension-feeding cladoceran *Daphnia magna*. A partial residual analysis that used a general additive model procedure allowed us to statistically separate algal and detrital carbon effects on *Daphnia* growth without physically disturbing the natural POM composition. We also compared the effects of seston collected from different habitat types and seasons on *Daphnia* growth in the laboratory.

All investigated habitats were situated in the Sacramento-San Joaquin River Delta and Suisun Marsh, the upstream portion of the San Francisco Estuary in central California. Herein, we will collectively refer to this part of the estuary as the "Delta." The Delta consists of a multitude of interconnected channels, wetlands, floodplains, and shallow lakes. Dry land in the Delta is intensely farmed and protected by levees. Water depths vary from <1 to >15 m. Delta hydrology is influenced by river inputs, various types of exports and diversions, outflow into San Francisco Bay, and tides. The diverse community of suspension feeders in the Delta consists of planktonic and benthic organisms, including several *Daphnia* species and other cladocerans, calanoid copepods, and bivalves such as the introduced clam *Potamocorbula amurensis*. A recent decline in phytoplankton biomass and some zooplankton species in large portions of this system has been linked in part to increased grazing pressure by *P. amurensis* (Jassby et al. 2002). For a more complete description of the system, current problems, and restoration efforts, see Jassby and Cloern (2000).

## Materials and methods

Study sites were chosen to represent different habitat types with different seston sources (Fig. 1). As a representative of tidal "river channel" habitat, currently the dominant habitat type in the Delta, we chose the Sacramento River at Rio Vista (A) and Sherwood Harbor (B) and the San Joaquin River at Twitchell Island/Fishermen's Cut (C), all on the northern shores. These downstream channel sites integrate POM from a large variety of upstream sources.

In contrast, Mildred Island (F), a shallow lake (mean depth 5 m) that was formerly a leveed island in the south-central Delta, has a longer residence time (2–4 d, Monsen 2001) and the potential for a more phytoplankton-derived seston pool. Our sampling station was situated in the middle of a cove on the west side of this "flooded island" habitat.

Suisun Slough (G) and Cut-Off Slough (H) are two shallow sloughs in Suisun Marsh, a tidal marsh that is part of Suisun Bay. With 236 km<sup>2</sup> of marsh land and 121 km<sup>2</sup> of bays and sloughs, Suisun Marsh provides the largest remaining "tidal marsh" habitat in the Bay-Delta system and is one of the largest tidal marshes in the contiguous United States (CDWR 2001). With its dominant tule growth (*Scirpus* spp.), it is reminiscent of the original state of much of the Delta before 1850. Marsh plants likely contribute significantly to its POM pool.

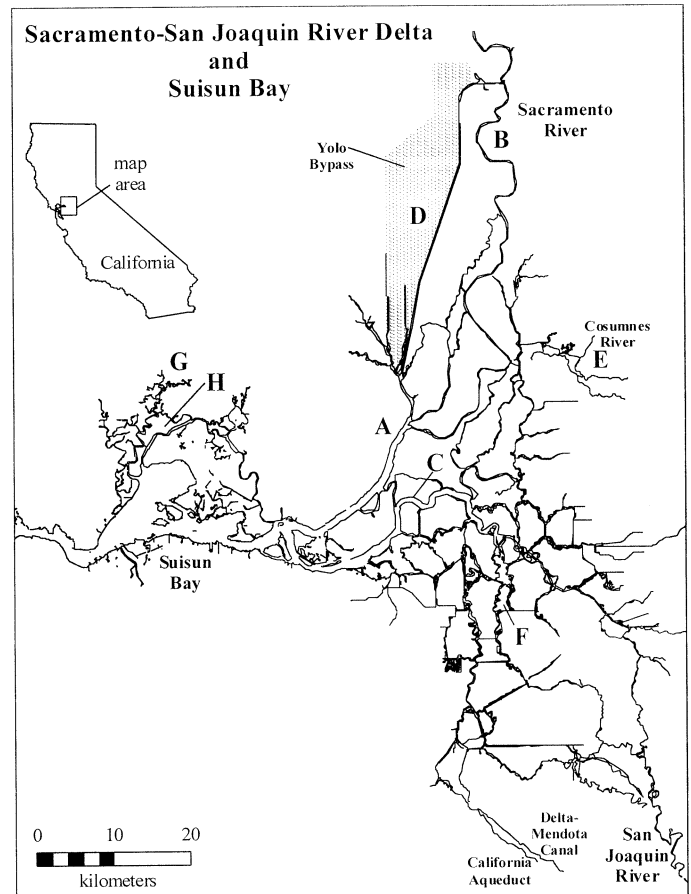


Fig. 1. Sampling sites in the San Francisco Estuary. (A) Sacramento River at Rio Vista; (B) Sacramento River at Sherwood Harbor; (C) San Joaquin River at Twitchell Island; (D) Yolo Bypass; (E) Cosumnes River floodplain; (F) Mildred Island; (G) Suisun Slough; and (H) Cut-Off Slough.

Another type of shallow water habitat formerly prevalent in the Delta is "floodplain" habitat. This habitat type is inundated only during a relatively short period in late winter and early spring. During this time, it exhibits great spatial variability in productivity. As a consequence, we investigated spatial rather than seasonal variation in *Daphnia* food resources in this habitat type. We included 11 sites in two floodplain areas in our study. These sites differed in depth, residence time, distance from the river channel, and, in some cases, source water. Five floodplain sites were in a small area situated next to the Cosumnes River (E, wetted area <1 km<sup>2</sup>), the last unregulated major tributary to the Delta. Six additional sites were situated within the Yolo Bypass (D), the largest floodplain habitat in the Bay-Delta system (wetted area 239 km<sup>2</sup>). A former natural floodplain, it is now leveed and highly regulated to convey excess flows from several streams including the Sacramento River and provides flood protection for the City of Sacramento and surrounding areas.

We conducted 18 laboratory growth assays according to procedures described by Müller-Navarra and Lampert (1996). During each growth assay, we concurrently fed natural seston contained in freshly collected Delta water sam-

ples from three to four sites per assay or cultured algae as a reference treatment (*Scenedesmus acutus*) to laboratory-raised *D. magna*. *D. magna* are deemed nonselective suspension feeders foraging on particles  $<40\ \mu\text{m}$  (Lampert 1987). They are often used as test and model organisms in freshwater ecology, including evaluations of food quality. The relatively high salt tolerance of *D. magna* expands their utility as test organisms into estuarine systems (Schuytema et al. 1997). *D. magna* occurs in the Delta, albeit not as a dominant species. On the basis of these characteristics, we chose *D. magna* as an appropriate model organism exemplifying the response of suspension-feeding zooplankton to varying seston food quality in this system. The *Scenedesmus* treatment served as a reference treatment of well-characterized and constant nutritional quality (see below). *S. acutus*, a common laboratory food organism for *Daphnia*, is considered to be of “medium-high” food quality for *Daphnia* and has been used in many laboratory investigations of algal food quality (Brett et al. 2000).

The growth assays were conducted from January 1999 through May 2000. Habitat types were sampled at least once per season. In the Delta, flow conditions and water temperatures show marked seasonal variations. These variations potentially affect seston concentrations and composition. Sampling was timed to capture these variations.

The assays were set up by use of a flow-through system to avoid changes in food quantity. Site water was renewed daily to avoid deterioration of food quality. Temperature ( $20^\circ\text{C}$ ) and light conditions (16 h light: 8 h dark) were kept constant to permit comparisons among assays. Assays were conducted by incubating 3-d-old *D. magna* born within 12 h of each other for 4 d in replicated flow-through chambers that continuously received site water or cultured *S. acutus* ( $1,000\ \mu\text{g L}^{-1}\ \text{C}$ ). This allowed development of their first clutch by the end of the experiment under favorable food conditions. Experimental organisms (*S. acutus* and *D. magna*) were raised under nonlimiting conditions in chemostat and batch cultures, respectively. At the start of the experiment, a subsample of juvenile *Daphnia* was dried and weighed to obtain initial weights. POM constituents (described below) were measured daily in the sample water and the reference algae culture. At the end of the experiment, the daphnids were harvested from the flow-through chambers and their final weights recorded as dry weights.

During each day of the 4-d growth assays, we collected near-surface water samples with a Van Dorn water sampler or a bucket. Starting with assay 8 (July 1999), specific conductance at the sampling sites was measured with a YSI 85 conductivity meter. We used 12- and 20-liter polyethylene bottles covered with insulated hoods to transport the water samples to the laboratory. Prior to filling, the bottles were soaked in dilute HCl and thoroughly rinsed with distilled water and with sample water. In most cases, water was screened through a  $243\text{-}\mu\text{m}$  Nitex screen while filling the transport bottles to remove mesozooplankton and large detritus. In the laboratory, the water was screened three more times through  $243\text{-}$  (50 samples) or  $30\text{-}\mu\text{m}$  (17 samples) Nitex screens to obtain  $<243\text{-}$  (“total”) and  $<30\text{-}\mu\text{m}$  (“edible”) seston size fractions. Comparisons between  $<243\text{-}$  and  $<30\text{-}\mu\text{m}$  seston size fractions were conducted to assess po-

tential mechanical interference of larger particles with *Daphnia* feeding. Subsamples of the screened sample water were placed in thoroughly washed and autoclaved Erlenmeyer flasks for use in the growth assays or processed for sample analysis.

For analysis of particulate organic carbon (POC), fresh seston samples were drawn onto precombusted 13-mm glass fiber filters (GF-AE). The filters were dried at  $60^\circ\text{C}$ , acidified in an acidic atmosphere overnight to remove inorganic carbon, and dried again. They were then wrapped in tin capsules and processed by the University of California at Davis stable isotope facility by use of a Europa Scientific Hydra 20/20 continuous-flow Isotope Ratio Mass Spectrometer (IRMS). Chlorophyll *a* concentrations were determined according to procedures recommended by Marker et al. (1980). Samples for Chl *a* analysis were drawn onto 47-mm glass-fiber filters (GF-C). The filters were frozen at  $-20^\circ\text{C}$  for at least 48 h and extracted with methanol in the dark at  $4^\circ\text{C}$  for 24 h. Chl *a* concentrations in the extracts were measured with a Turner 10 AU fluorometer by use of the fluorometric method with acid correction for degradation products.

To evaluate seston quality independent of food quantity effects, we compared the Delta growth assay results with the amount of *Scenedesmus* carbon necessary to achieve similar growth rates under the same standardized experimental conditions (Müller-Navarra and Lampert 1996). These “*Scenedesmus* equivalent carbon” (SEC) levels were calculated from the mathematical relationship between *Daphnia* growth rates and *Scenedesmus* carbon concentrations obtained in an additional laboratory growth assay. In this assay, we fed *S. acutus* cultures ranging from 50 to  $2,000\ \mu\text{g L}^{-1}\ \text{C}$  to the identical *D. magna* clone used in the Delta growth assays under the same experimental conditions. We compared SEC levels with estimates of phytoplankton carbon concentrations (PHY C) in our samples by converting Chl *a* concentrations using a C:Chl *a* ratio of 35, which has been used elsewhere as a characteristic value for this system (Canuel et al. 1995). Although this ratio is actually highly variable in practice, both within and among systems, we use it only in this context and consider the ramifications of its variability.

*Daphnia* growth rates were calculated as the logarithmic increase in dry weight over the 4-d duration of the experiment. We used an asymptotic model with offset to describe the relationship between growth rate and seston components (Ivlev 1961). Model parameters were estimated with the Levenberg-Marquardt algorithm, a method commonly used for nonlinear curve optimization. We also examined the effect of each of Chl *a* and POC on *Daphnia* growth, with the effect of the remaining variable removed. Specifically, we used a general additive model procedure with splines as smoothers and examined the resulting partial residual plots for the two predictor variables, Chl *a* and POC (Hastie and Tibshirani 1990). On the basis of the number of data points available, the smoothing splines had 3 and 2 degrees of freedom for the  $<243\text{-}$  and  $<30\text{-}\mu\text{m}$  size fractions, respectively. A two-way analysis of variance (ANOVA) was used to look for effects of habitat and season on growth. Subsequently, the pairwise effects of habitat on growth were assessed by calculation of differences in mean growth rates between hab-



Table 1. Median POC and Chl *a* concentrations in the <243- $\mu\text{m}$  seston size fraction and related estimates for Delta habitats and seasons. SEC, *Scenedesmus* equivalent carbon concentrations associated with observed *Daphnia* growth rates; PHY C, phytoplankton carbon concentrations estimated from Chl *a* concentrations. All concentrations are in  $\mu\text{g L}^{-1}$ . For SEC and PHY C estimation, see Materials and methods section.

Habitat	Season			
	Winter	Spring	Summer	Fall
<b>POC</b>				
River	969	805	841	1,373
Flood plain	1,312	1,801	—	—
Flooded island	382	845	749	953
Tidal marsh	2,902	2,555	2,682	2,323
<b>Chl <i>a</i></b>				
River	3.3	4.4	3.2	2.8
Flood plain	5.0	7.6	—	—
Flooded island	2.6	9.1	3.1	3.1
Tidal marsh	14	15	6.3	8.4
<b>SEC</b>				
River	108	181	61	193
Flood plain	178	773	—	—
Flooded island	140	546	113	1,321
Tidal marsh	1,014	1,001	600	558
<b>PHY C</b>				
River	116	154	112	98
Flood plain	175	266	—	—
Flooded island	91	319	109	459
Tidal marsh	473	525	221	294

it pairs and simultaneous 95% confidence intervals by use of the Tukey-Kramer method (Hsu 1996).

## Results

The two food-related seston constituents measured in our growth experiments, POC and Chl *a*, were highly variable among different habitats and seasons. POC and Chl *a* concentrations in all seston samples varied by more than an order of magnitude from  $\sim 330$  to  $3,800 \mu\text{g L}^{-1}$  POC and  $1.4$  to  $45 \mu\text{g L}^{-1}$  Chl *a*. The two size fractions exhibited a similar degree of variation. Tidal marsh habitat was generally highest in POC and highest or second highest in Chl *a* (Table 1). The highest Chl *a* value ( $45 \mu\text{g L}^{-1}$ ) was measured in a <243- $\mu\text{m}$  seston sample from the flooded island habitat in spring 2000. It was  $20 \mu\text{g L}^{-1}$  higher than the next highest value and  $36 \mu\text{g L}^{-1}$  higher than the Chl *a* concentration measured in the <30- $\mu\text{m}$  seston size fraction of the same sample. This unusually high value was associated with a bloom of the filamentous diatom *Skeletonema subsalsum*. This species was responsible for 79% of all algal cells and 97% of algal biovolume in the <243- $\mu\text{m}$  seston fraction at this time. The 30- $\mu\text{m}$  screen effectively reduced the number of *Skeletonema* filaments in the <30- $\mu\text{m}$  size fraction. The unusual bloom sample was omitted from all statistical analyses.

Mean and median concentrations in the <243- $\mu\text{m}$  size

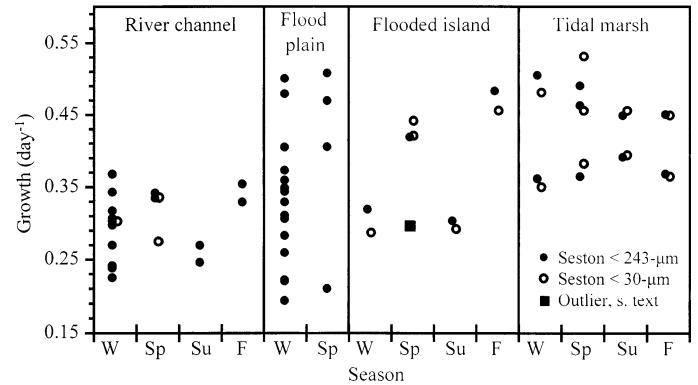


Fig. 2. Seasonal and habitat-related variation in *Daphnia* growth rates under standardized experimental conditions. W, winter; Sp, spring; Su, summer; and F, fall.

fraction were  $1,435$  and  $1,129 \mu\text{g L}^{-1}$  POC and  $6.0$  and  $3.8 \mu\text{g L}^{-1}$  Chl *a*, respectively ( $n = 49$ ). Mean and median concentrations in the <30- $\mu\text{m}$  size fraction were of similar magnitudes, with  $1,652$  and  $1,141 \mu\text{g L}^{-1}$  POC and  $7.3$  and  $6.3 \mu\text{g L}^{-1}$  Chl *a*, respectively ( $n = 17$ ). Overall, POC and Chl *a* values were significantly and linearly related in the total seston size fraction ( $r^2 = 0.49$ ,  $n = 49$ ,  $P < 0.001$ ) but not in the <30- $\mu\text{m}$  seston size fraction ( $r^2 = 0.18$ ,  $n = 17$ ,  $p = 0.09$ ). Much of the variability in POC was thus independent of Chl *a*.

*Daphnia* growth rates measured in our growth assays at a constant temperature of  $20^\circ\text{C}$  varied from  $0.19$  to  $0.53 \text{ d}^{-1}$  in response to the different seston sources and size fractions (Fig. 2). In the algal reference treatments with  $\sim 1,000 \mu\text{g L}^{-1}$  *Scenedesmus*-C, *Daphnia* always grew at near-maximum growth rates, averaging  $0.45 \pm 0.05 \text{ d}^{-1}$  ( $n = 18$ ), which indicates healthy *Daphnia* cultures. Initial *Daphnia* weights in the growth assays were  $0.04 \pm 0.01 \text{ mg individual}^{-1}$ . Specific conductance measured in the sample water and algal reference treatments never exceeded  $7.5 \text{ mS m}^{-1}$  and was usually  $< 1 \text{ mS m}^{-1}$ —i.e., well within the salt tolerance range of *D. magna* (Schuyttema et al. 1997).

The 17 parallel treatments of size fractionated samples (<30- vs. <243- $\mu\text{m}$ ) generally produced similar growth results. According to a matched *t* test, differences in mean values were not statistically significant ( $t = -0.16$ ,  $P = 0.87$ ); the overall mean difference was only  $0.0015 \text{ d}^{-1}$ , with a 95% confidence interval ranging from  $-0.022$  to  $0.018 \text{ d}^{-1}$ . Subsequent tests were therefore conducted with the <243- $\mu\text{m}$  size fraction, which had more observations (49 cases). *Daphnia* exhibited significantly lower growth only on total seston from Mildred Island in spring 2000 during the *S. subsalsum* bloom (Fig. 2, square symbol).

We fitted the *Daphnia* growth results to the two measured POM constituents, POC and Chl *a*, using an asymptotic model (Fig. 3). We found that, although these constituents were significantly related to *Daphnia* growth for both size fractions of Chl *a* and the <30- $\mu\text{m}$  size fraction of POC, the fit was much better for Chl *a* ( $r^2_{<243\mu\text{m}} = 0.79$ ,  $n = 49$ ,  $P < 0.001$ ;  $r^2_{<30\mu\text{m}} = 0.87$ ,  $n = 17$ ,  $P < 0.001$ ) than for POC ( $r^2_{<243\mu\text{m}} = 0.45$ ,  $n = 17$ ,  $P < 0.001$ ). Using the same nonlinear regression technique, we failed to reach convergence for

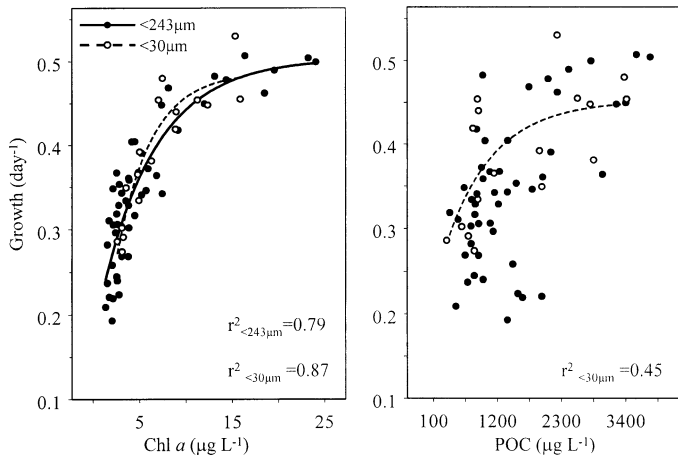


Fig. 3. Nonlinear regression results of *Daphnia* growth rates against size-fractionated Chl *a* and POC concentrations. Filled circles and solid line: seston <243  $\mu\text{m}$ ; open circles and dotted line: seston <30  $\mu\text{m}$ . Convergence was not achieved for POC <243  $\mu\text{m}$ , and no line could be fitted.

the <243- $\mu\text{m}$  size fraction of POC even when an algorithm was used that did not require choosing starting values. The *Daphnia* growth rate increased most dramatically with increasing Chl *a* concentrations between 1 and 10  $\mu\text{g L}^{-1}$ .

We also fitted generalized additive models and performed partial residual analyses, examining the effect of Chl *a* and POC on *Daphnia* growth rates, each with the effect of the other removed (Fig. 4). These analyses showed highly significant relationships for the effects of Chl *a* ( $P_{<243\mu\text{m}} < 0.001$ ,  $n = 49$ ;  $P_{<30\mu\text{m}} = 0.012$ ,  $n = 17$ ) but not for the effects of POC ( $P_{<243\mu\text{m}} = 0.812$ ,  $n = 49$ ;  $P_{<30\mu\text{m}} = 0.196$ ,  $n = 17$ ) on *Daphnia* growth. The partial residual curves for Chl *a* effects on *Daphnia* growth resembled saturation growth curves, whereas for POC effects they did not resemble any common biological response curves.

Comparing total POC levels with carbon levels of cultured *S. acutus* supporting equal *Daphnia* growth rates, we found that usually a much smaller concentration of *Scenedesmus* equivalent carbon (median SEC, 23% of Delta POC <243  $\mu\text{m}$ ; SEC range, 7%–139% of Delta POC <243  $\mu\text{m}$ ) was required to achieve the growth rates observed in our Delta assays (Table 1). In contrast, PHY C concentrations in the Delta assays estimated by use of a PHY C:Chl *a* ratio of 35 were more similar to and even below the calculated SEC concentrations. POC quality appeared to surpass that of *Scenedesmus* only in one case: flooded island habitat in fall. This was also the case in which phytoplankton contributed the most carbon (nearly 50%) to POC. In general, phytoplankton contribution to POC in the <243- $\mu\text{m}$  size fraction was low in tidal marsh, river channel, and floodplain habitats (median, 13%) but higher in the flooded island habitat (median, 31%).

Overall, habitat type ( $P = 0.002$ ) but not season ( $P = 0.217$ ) had a strong effect on growth rates, according to a two-way ANOVA. The pairwise differences in growth for different habitat types were significant only when comparing tidal marsh with either floodplain or river channel habitat. In both cases, tidal marsh supported faster growth (Fig. 5).

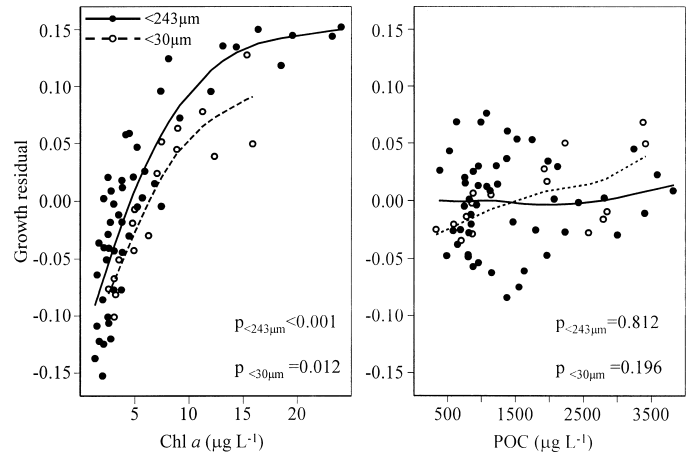


Fig. 4. Partial residual plots of Chl *a* and POC effects on *Daphnia* growth by use of a general additive model procedure with splines as smoothers. (Left) Growth residual is the partial residual of *Daphnia* growth after removing the effects of POC. (Right) Growth residual is the partial residual of *Daphnia* growth after removing the effects of Chl *a*. For symbols and lines, see Fig. 3.

Floodplain seston showed great spatial variation in nutritional quality, whereas seston from the flooded island produced seasonally variable growth rates. When Chl *a* was used as a covariate, there were no longer any significant differences between habitats.

## Discussion

The variability of more than an order of magnitude of POC and Chl *a* concentrations in our experiments captured the Delta's natural variability in these seston constituents (CDWR 1996). Although occasional phytoplankton blooms (like that of *S. subsalsum*) are observed in the Delta (Jassby and Powell 1994), the contribution of detrital carbon to seston usually far outweighs that of algal carbon. Moreover, POC constitutes on average only a very small fraction (1%–4%) of total seston particles (Schemel et al. 1996). In general, Chl *a* is related positively with suspended particle concentration in the Delta. Using historical data (1968–1998) collected throughout the Delta by the California Department of Water Resources (CDWR) and the United States Bureau of Reclamation according standard methods (CDWR 1996), we found that Chl *a* and total suspended solids were positively correlated at all stations ( $r = 0.0047$ – $0.54$ ,  $n = 337$ – $505$ ,  $P < 0.05$  in 20 of 24 stations). Seasonal fluctuations are likely due to high tributary-borne sediment loads in winter and wind resuspension in shallow areas in spring and summer (Cuetara et al. 2001; Jassby et al. 2002). Suspension-feeding consumers thus have to contend with a large amount of potentially inedible or nutritionally inferior particles in this system.

Substrates collected from all investigated habitats allowed the test organism *D. magna* to grow, indicating food concentrations above threshold levels for somatic growth for this low-threshold species (Gliwicz 1990). However, *D. magna* growth in many of our assays was substantially below the maximum potential growth rate. This suggests that, in many

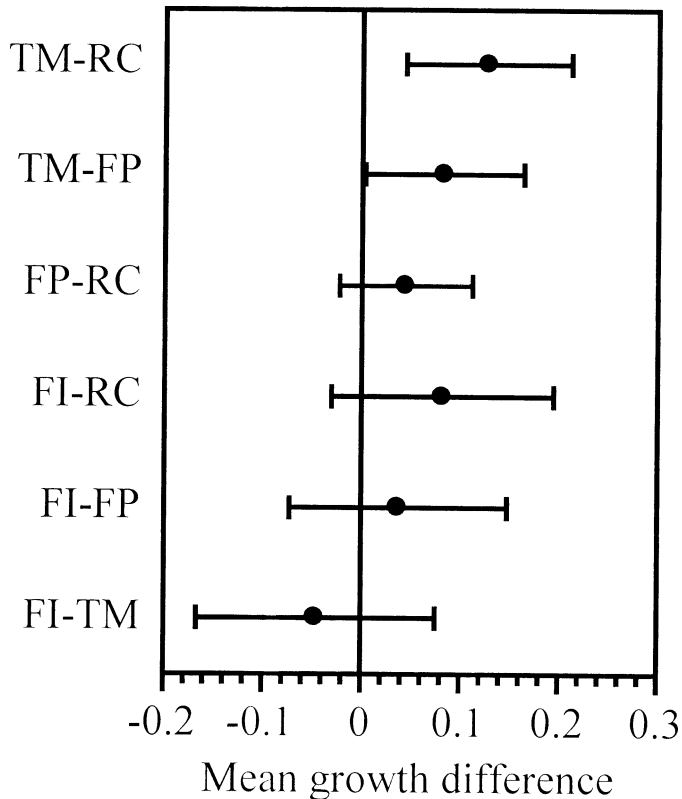


Fig. 5. Pairwise comparisons of habitat effect on *Daphnia* growth. Each point represents the difference in mean *Daphnia* growth between two habitats. The error bars are 95% confidence intervals for each difference. FP, floodplain; FI, flooded island; RC, river channel; TM, tidal marsh.

cases, insufficient amounts of a critical seston component may have been accessible to the test organisms under the standardized experimental conditions.

The strong positive relationship between *D. magna* growth and Chl *a* across all habitats compared to the much weaker relationship with POC compellingly suggests that the growth-limiting factor (or factors) is associated with phytoplankton rather than with total POC (Fig. 3). However, these relationships do not allow conclusions about the comparative nutritional roles of phytoplankton versus detrital carbon, because both types of carbon contribute to POC. Phytoplankton POC cannot be experimentally separated from detrital POC without disturbing the natural POM properties because of overlapping size ranges. We thus used a statistical technique—generalized additive modeling combined with partial residual analysis—to separate effects of phytoplankton carbon indicated by Chl *a* and bulk detrital POC on *Daphnia* growth. The shapes of the resulting curves were a product of the applied smoothing procedure rather than dictated by a specific model. Remarkably, the shapes of the resulting Chl *a* partial residual curves closely resemble the nonlinear regression curves of Chl *a* versus growth for both seston size fractions. In contrast, there are no obvious shapes associated with detrital POC, although the increasing trend for the <30- $\mu\text{m}$  POC size fraction may warrant further investigation.

The results from our statistical analyses indicate that bulk detrital POC is not nutritionally relevant in regulating *Daphnia* growth. It is possible, however, that there are some constituents of bulk detrital POC whose nutritional importance is masked by the overall poor quality of detrital particles. For example, in this study we do not distinguish between dead particulate matter and associated microorganisms. It has been well documented that microorganisms can be heavily grazed by zooplankton (Juergens 1994), and it is possible that microorganisms contribute important substances to zooplankton nutrition. Some evidence has suggested, however, that their nutritional quality for zooplankton is inferior to phytoplankton (Ederington et al. 1995). Although microbial organisms may play a greater role in copepod than in cladoceran nutrition, copepod egg production was found to be most closely related to Chl *a*: seston ratios in several European estuaries (Burdloff et al. 2000).

Varying Chl *a* concentrations explained ~80% of the variation in *D. magna* growth in our assays. The relatively small unexplained variability might arise from several factors. First, Chl *a* is not an essential nutritional factor. As a marker for the phytoplankton fraction of POM, it is merely a surrogate for a food component. There may be a nutritional factor or a combination of factors more predictive of *Daphnia* growth. Potential factors include mineral nutrient content and biochemical compounds such as essential fatty acids (Sterner and Schulz 1998). Factors not related to the varying chemical food quality of seston include those that influence the animals' ability to use potential food resources efficiently. Most important among these is probably the high amount of mineral particles interfering with both collection and digestion of nutritious POM constituents in Delta waters: overcollection of large amounts of inert particles by suspension feeders leads to increased particle rejection and defecation rates and decreased filtration, which results in reduced feeding and digestion efficiencies. This type of interference has been shown in a number of field and laboratory studies (e.g., Hart 1988). It is particularly pronounced when suspended particle concentrations are high and algal concentrations are low (Kirk 1991), as is the case in the Delta as well as in many other estuaries and reservoirs. Inefficient grazing can also result from inappropriate POM size, rendering particles inedible. In our study, removing particles >30  $\mu\text{m}$  resulted in an improvement of the Chl *a*-growth relationship by 8% of the variance explained, although the differences in growth rates between the two size fractions were generally not statistically significant. The only significant difference was found after the removal of a large amount of *Skeletonema* filaments from the seston collected in Mildred Island in spring 2000. These filaments apparently strongly interfered with efficient feeding by *Daphnia*. Other kinds of inedibility, toxicity, and slight differences in experimental conditions between experiments may also have contributed to the unexplained variation. Remarkably, in spite of the widely documented contamination of Delta water and sediments with pesticides and heavy metals (e.g., Hinton 1998), these toxins apparently never greatly inhibited *Daphnia* growth in our assays.

The comparison of the results from our growth assays with SEC levels showed that usually much more Delta POC

than *S. acutus* carbon was needed to achieve similar growth rates under the same standardized experimental conditions. This indicates the overall poor nutritional quality of Delta seston compared with *Scenedesmus*. Delta seston was of better nutritional quality than cultured *Scenedesmus* only in the flooded island habitat during fall, when phytoplankton constituted an unusually large proportion of POM. This is similar to the results of a study by Müller-Navarra and Lampert (1996), in which lake seston exceeded *Scenedesmus* food quality for *Daphnia galeata* growth in fall. In general, SEC levels corresponded much more closely to the estimated Delta PHY C levels than to the measured POC concentrations. This indicates that Delta phytoplankton is not only very important in regulating *Daphnia* growth in this system but that it is generally also of good nutritional quality across all habitats and seasons. This is a somewhat surprising result in light of the substantial physical differences between Delta habitats and seasons examined in this study and the overall high grazing pressure by planktonic and benthic suspension feeders on Delta phytoplankton (Jassby et al. 2002).

There are, however, several caveats to the interpretation of the SEC-related results. First, Delta carbon concentrations generally exceeded the incipient limiting level (ILL; McMahon and Rigler 1963) for *D. magna* of  $\sim 300\text{--}400 \mu\text{g L}^{-1}$  edible carbon (Bohrer and Lampert 1988). Carbon in excess of the ILL may not have been ingested and assimilated by the daphnids, leading to an underestimation of Delta POM and overall seston food quality compared with that of *Scenedesmus*. Second, the high amounts of inert inorganic suspended particles in the Delta most likely interfered with efficient feeding on nutritious particles, as discussed above. Similar to the ILL effect, this interference effect may also lead to underestimation of the nutritional quality of Delta POM compared with *Scenedesmus*. Unlike the ILL effect, however, it does not affect the comparative nutritional evaluation of total seston because inorganic suspended particles are an integral part of seston. Moreover, the interference effect alleviates the ILL effect because *Daphnia* in our assays likely remained carbon-limited at POC levels higher than the previously determined ILL because of the high concentrations of interfering inorganic particles effectively "diluting" the amount of available POC. Last, the comparison between PHY C estimated from Chl *a* concentrations and *Scenedesmus* carbon effects on *Daphnia* growth depends greatly on the choice of PHY C:Chl *a* ratio. This ratio can be highly variable depending on algal community composition and environmental conditions. Although our choice of a fixed PHY C:Chl *a* ratio is consistent with published ratios for this system (Canuel et al. 1995) and within the range of results from a more recent Delta seston field survey (W. Sobczak et al. pers. comm.), it does not account for variability. Consequently, all PHY C-related results should be viewed with caution.

In summary, phytoplankton in the Delta appears to be a far more important food resource for suspension feeders than detritus. This result complements findings from carbon tracer studies (e.g., Finlay 2001; Grey et al. 2001) by showing the importance of phytoplankton in detritus-rich systems not just as a quantitative carbon source but also in regulating consumer growth. Similar to results of lake enclosure experi-

ments that have used carbon isotope additions (Hessen et al. 1990), detritus may augment and even contribute a considerable amount of carbon to the zooplankton diet in the Delta. However, a growth factor (or factors) associated with phytoplankton appears to become limiting at Chl *a* concentrations below  $\sim 10 \mu\text{g L}^{-1}$ .

Like many other low-elevation rivers and estuaries, the Delta has undergone profound geomorphologic alterations. These alterations include extensive draining of its once widespread wetlands and shallow water habitats and confinement of a large portion of its water mass to deep channels (CALFED 2000). These developments have been accompanied by ecological changes such as shifts in aquatic community composition and dramatic declines in population densities of many native species including fish (Bennett and Moyle 1996) and zooplankton species (Kimmerer and Orsi 1996). Chl *a* levels have also decreased in the Delta during the last three decades and are now commonly  $<10 \mu\text{g L}^{-1}$  (Jassby et al. 2002). The results from our study suggest the decline in algal food resources as one possible mechanism responsible for the simultaneously observed decline in consumer species, at least at the level of primary consumers in the water column. A further drop or increase in Chl *a* levels could have dramatic impacts on consumer dynamics.

In our study, Chl *a* levels differed markedly among habitat types. *Daphnia* growth rates varied accordingly and were significantly higher in growth assays with tidal marsh seston than with seston from the river channel or floodplain sites. Although our results suggest that this is mostly related to higher phytoplankton concentrations in the tidal marsh sites, detrital quality may also have been higher in these sites. Presumably, much of the detrital matter in the tidal marsh sloughs is derived from marsh plants. This "fresh" detritus may be more bioavailable than the older detritus of terrestrial origin predominant in low-elevation rivers near their mouths (Raymond and Bauer 2001). Tidal marsh and several floodplain sites provided the best growth substrates for *Daphnia* during late winter and early spring, the time period favored by native Delta fishes for spawning and rearing (Sommer et al. 2001). Preservation and restoration of tidal marshes and floodplains may thus help maintain and restore important ecosystem functions such as the production of a sufficiently nutritious food base for native consumers.

The flooded island habitat type provided good food resources for zooplankton growth in spring and fall, although overall growth rates were statistically indistinguishable from the other sites. Successional zooplankton and phytoplankton dynamics similar to those commonly observed in lakes (Sommer et al. 1986) may have been responsible for the observed seasonal seston variations in this shallow lake. However, food resources in this habitat were inferior to those of the tidal marsh and several floodplain sites during the late winter/early spring period critical for juvenile native fishes. Furthermore, because of its longer residence time, nutritionally inferior phytoplankton blooms may be more common in this habitat type.

Similar to the Delta, many low-elevation river systems receive large inputs of terrigenous carbon and exhibit net heterotrophy (Cole and Caraco 2001). Nevertheless, as our results indicate, the scarcer aquatic food sources may regu-



late metazoan consumer production in such systems. This is in contrast to results from other studies of cross-system transfers from more to less productive habitats (Polis et al. 1996), where allochthonous subsidies played a large role in controlling food web processes. Reasons for the different ecosystem responses may include differences in allochthonous matter quality, POM residence time in the receiving system, and the trophic role of the primary recipient organisms. Terrigenous POM may already be severely degraded during its passage through the Delta's large watershed and reach the Delta in a state of insufficient nutritional quality for metazoan consumption. Sobczak et al. (2002) found that POM bioavailability in the Delta is low even for microorganisms: only a small portion of POM is metabolized by microorganisms within the short residence time of this system. Because of the nutritional inferiority of microorganisms for pelagic metazoan consumers (Ederington et al. 1995) and transfer losses in the microbial food web, most of this carbon may not be transferred to pelagic metazoa and thus have little influence on pelagic food web processes (Jassby and Cloern 2000).

In conclusion, our study shows the importance of phytoplankton in regulating the growth of pelagic suspension feeders such as *D. magna* in detritus-rich, turbid systems. Although detrital carbon may represent an important subsidy for microbial communities and contribute greatly to carbon budgets and community respiration, it may be much less important for regulation of metazoan food web dynamics in these systems. Overall, seston food quality for suspension feeders in the Delta is low because of the large amounts of low-quality detritus. Inert inorganic particles probably also contribute to low seston food quality. In contrast, the phytoplankton component of Delta seston is generally of good nutritional quality and limits *Daphnia* growth under standard experimental conditions at concentrations  $<10 \mu\text{g L}^{-1}$  Chl *a*. Differences in potential growth rates between habitats are strongly related to differences in phytoplankton concentrations and are largely independent of differences in detrital carbon. From a restoration perspective, the results of this study emphasize the importance of tidal marsh and floodplain preservation and restoration as relatively food-rich areas for pelagic primary consumers.

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Received: 17 September 2001

Accepted: 15 April 2002

Amended: 25 April 2002