

Southern Illinois University Carbondale
OpenSIUC

Publications

Department of Zoology

12-2003

Algal vs. Macrophyte Inputs to Food Webs of Inland Saline Wetlands

E. Andrew Hart

James R. Lovvorn

Southern Illinois University Carbondale

Follow this and additional works at: http://opensiuc.lib.siu.edu/zool_pubs

© 2003 by the Ecological Society of America

Published in *Ecology*, Vol. 84, No. 12 (December 2003) at doi: [10.1890/02-0629](https://doi.org/10.1890/02-0629)

Recommended Citation

Hart, E. A. and Lovvorn, James R. "Algal vs. Macrophyte Inputs to Food Webs of Inland Saline Wetlands." (Dec 2003).

This Article is brought to you for free and open access by the Department of Zoology at OpenSIUC. It has been accepted for inclusion in Publications by an authorized administrator of OpenSIUC. For more information, please contact opensiuc@lib.siu.edu.

ALGAL VS. MACROPHYTE INPUTS TO FOOD WEBS OF INLAND SALINE WETLANDS

E. ANDREW HART AND JAMES R. LOVVORN¹

Department of Zoology, University of Wyoming, Laramie, Wyoming 82071 USA

Abstract. Invertebrate food webs in wetlands were traditionally thought to be fueled mainly by decaying macrophytes, but recently it has been recognized that microalgae may be more important. In particular, the paradigm that shredders of vascular plant litter dominate food web processes may not apply to many wetlands where shredders are rare and microalgae more abundant. This issue is complicated by potential consumption of flocs of dissolved organic matter (DOM) released from living plants, and of exopolymer secretions (EPS) from both autotrophic and heterotrophic microbes. In Wyoming, we used gut contents and stable isotopes to investigate organic matter sources for the dominant invertebrates in oligosaline (0.5–5 g/L total dissolved solids) and mesosaline (5–18 g/L) wetlands. We examined the trophic importance of microalgae vs. macrophytes in wetlands with and without emergent vegetation (*Scirpus acutus*), with different growth forms and species of submersed plants (*Chara* spp. vs. *Potamogeton pectinatus*), with dominance by different microalgal types (phytoplankton, epiphyton, epipelon), and with different primary consumers (mainly amphipods vs. chironomid larvae). In all wetlands studied, guts of the major primary consumers contained little or no macrophyte tissue, but rather mostly amorphous detritus (organic particles with no recognizable cellular structure). Values of $\delta^{13}\text{C}$ indicated that organic matter entering foodwebs was not from submersed macrophytes, but that emergent plants might be a source of DOM or EPS in amorphous detritus. However, in some wetlands, amphipods eating mainly amorphous detritus had the same $\delta^{13}\text{C}$ values as chironomids eating a much higher fraction of diatoms, indicating that amorphous detritus was derived mainly from diatoms. Patterns of temporal change of $\delta^{13}\text{C}$ in consumers, seston, and emergent plants supported this interpretation. We conclude that microalgae rather than macrophytes provided most organic matter for these food webs via amorphous detritus. Amorphous detritus is often thought to have poor nutrient quality and low assimilation efficiency, but this idea may not be true if amorphous detritus is largely flocs of labile DOM/EPS. Our results suggest that characterizing the origin and nature of amorphous detritus is key to understanding variations in macroinvertebrate production among saline wetlands and a broad range of wetland types.

Key words: *algal forms; amorphous detritus; dissolved organic matter; exopolymer secretions; invertebrate food webs; invertebrate gut contents; macrophytes; organic matter sources; saline wetlands; stable isotopes; wetland food webs.*

INTRODUCTION

In nontidal wetlands, invertebrate food webs were traditionally thought to be fueled mainly by decomposing macrophyte tissue, especially of emergent plants (Murkin 1989, Batzer and Wissinger 1996, Mitsch and Gosselink 2000). Accordingly, basic texts, as well as wetland creation and restoration manuals, generally treat food webs in nontidal wetlands as detritus-based (e.g., Marble 1992, Horne and Goldman 1994, Hammer 1997, Mitsch and Gosselink 2000). More recently attention has shifted to algae—despite lower standing stocks, the higher production and digestibility of microalgae might make them more important to invertebrate production (Campeau et al. 1994, de Szalay and Resh 1996, Goldsborough and

Robinson 1996, Euliss et al. 1999). For inland saline wetlands, microalgae might be especially critical because emergent plants are restricted by unstable water levels and high salinities; however, such wetlands usually contain submersed macrophytes (Hart and Lovvorn 2000). Identifying organic sources is complicated by potential consumption of flocs of dissolved organic matter (DOM) released by plants or algae while alive or in early decomposition (Mann 1988), and of exopolymer secretions (EPS) from algae and from microbes consuming different plant species (Decho 1990). These materials can form highly digestible amorphous detritus (organic particles with no recognizable cellular structures) that might increase the availability of macrophyte production. Both production and consumer use of macrophytes and microalgae can vary with community composition (Boschker et al. 1995, Currin et al. 1995, Kwak and Zedler 1997, Page 1997), and different types of saline wetlands differ in

Manuscript received 11 October 2002; revised 28 February 2003; accepted 7 March 2003; final version received 28 March 2003. Corresponding Editor: S. L. Kohler.

¹ Corresponding author. E-mail: lovvorn@uwoyo.edu

dominant macrophytes, microalgal forms, and invertebrates (Lovvorn et al. 1999, Hart and Lovvorn 2000). Thus, pathways and flows of macrophyte and microalgal carbon to different invertebrates are key to food web functions of different wetland types, and their ability to support diverse consumers at a range of trophic levels (Wollheim and Lovvorn 1995).

In wetlands of prairies and plains, the traditional focus on emergent macrophytes as the base of food webs stemmed largely from their obviously high biomass and production (Murkin 1989). With little direct herbivory, most macrophyte production accumulates through the growing season and enters the water as dead stems and leaves. Such wetlands were perceived as detritus-based systems in which secondary production depends mainly on organic input from senescent macrophytes. In such a situation, shredding macroinvertebrates are thought to play a vital role in invertebrate communities and organic matter cycling, by consuming coarse particulate organic matter (CPOM) such as leaf fragments and egesting fine particulate organic matter (FPOM) (Webster and Benfield 1986, Cummins et al. 1989, Cuffney et al. 1990). However, for many nonforested wetlands with few shredding invertebrates, the shredder paradigm has been questioned (Wissinger 1999). Much senescent emergent tissue is decomposed by fungi while the plants are still standing, before they enter the water and become available to aquatic invertebrates (Newell et al. 1995, Barlocher and Biddiscombe 1996). Thus, in prairie and plains wetlands, physical and microbial action may be far more important than shredders in processing macrophyte CPOM and generating FPOM.

Standing stocks of microalgae are usually much smaller than for macrophytes, but can turn over rapidly. In prairie and plains wetlands, total microalgal production can be comparable to that of macrophytes (Robinson et al. 1997, Hart and Lovvorn 2000) and algae are much more digestible (Mann 1988). In a model that parallels cyclic succession of macrophytes, Goldsborough and Robinson (1996) envisioned four wetland states, each dominated by a different form of microalgae: epipelton on and in sediments, epiphyton on macrophyte surfaces, phytoplankton in the water column, or metaphyton growing in mats. Secondary production was presumed to be linked to the dominant microalgal form, but the importance of each algal type to macroinvertebrates has not been widely examined.

In prairie and plains wetlands, attempts to discern the trophic role of microalgae for macroinvertebrates have included both stable isotope surveys and fertilization experiments. In prairie wetlands of Manitoba, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ indicated that macroinvertebrates did not consume metaphyton or submersed aquatic plants, but the significance of epiphyton, emergent macrophytes, and floating macrophytes (*Lemna minor*) could not be distinguished (Neill and Cornwell 1992). In North Dakota, $\delta^{13}\text{C}$ suggested that most invertebrates depended

on carbon derived from microalgae, with little contribution of emergent, submersed, or floating macrophytes (Euliss et al. 1999). Also in Manitoba, available foods were manipulated by reducing macrophyte litter, replacing fallen dead stems with polyurethane foam, and increasing algae by adding nutrients (Campeau et al. 1994). Results varied for different invertebrates, but the biomass of abundant chironomid larvae did not differ between treatments with foam vs. macrophyte stems. However, over the whole season, more chironomids emerged from treatments with real stems than from those with foam. Chironomids responded to nutrient-induced algal increases with earlier peak emergences. These studies raise several questions about the role of microalgae in secondary production. Is the relative importance of algae related to standing stocks of emergent or submersed plants of different species? Is the form of microalgae with dominant biomass the most important form (sensu Goldsborough and Robinson 1996)? Does the role of microalgae depend on the taxa of macroinvertebrates present?

In the Laramie Basin, Wyoming, we used stable isotopes and gut contents to examine the importance of macrophyte vs. algal inputs to food webs for two types of saline wetlands dominated by different macrophyte, microalgal, and invertebrate communities. The oligosaline wetlands (0.5–5 mg/L total dissolved solids, TDS) have peripheral stands of hardstem bulrush (*Scirpus acutus*) surrounding open water dominated by the low-growing macroalga *Chara* spp. Microalgal biomass and production are dominated by epiphyton growing on the surfaces of *Chara* (Hart and Lovvorn 2000), and primary consumer biomass is dominated mainly by amphipods (Wollheim and Lovvorn 1995, 1996). The mesosaline wetlands (5–18 g/L TDS) lack emergent plants and have a fringe of unvegetated mudflat often with a crust of salt; submersed macrophytes are mostly angiosperms with erect growth forms, mainly sago pondweed (*Potamogeton pectinatus*). Microalgal biomass and production are more evenly distributed between phytoplankton, epiphyton, and epipelton. Amphipods are uncommon in mesosaline wetlands, and chironomid larvae and zooplankton (copepods and cladocerans) dominate primary consumer biomass. Thus, we compared the trophic importance of microalgae vs. macrophytes between wetlands with and without emergent vegetation, with different growth forms and species of submersed macrophytes, with dominance by different microalgal types, and with different invertebrate communities.

METHODS

Use of stable isotopes to identify carbon sources and food web pathways is typically based on the assumptions that $\delta^{13}\text{C}$ changes by $<1\%$ and $\delta^{15}\text{N}$ by a mean of $\sim 3.4\%$ per trophic level (Fry 1991, Neill and Cornwell 1992). However, fractionation of ^{15}N can vary appreciably from this mean value in different situations

and for different trophic levels (Vander Zanden and Rasmussen 2001, Hart and Lovvorn 2002). Moreover, the mean of more than one food with different isotope values can erroneously indicate consumption of yet another item that is not eaten. Consequently, we used both gut contents and stable isotopes at different times in different wetlands to examine trophic relationships (Mihuc and Toetz 1994).

Macroinvertebrates, seston, epiphyton, plants, and sediments were collected in early June and mid-August 2000 in two oligosaline (George and Nelson) and two mesosaline wetlands (Creighton and Gibbs) in the Laramie Basin, Wyoming (Peck and Lovvorn 2001) (see see Plate 1). Samples were collected at three different sites per wetland and analyzed separately. Water depth at each site was ~ 0.5 m, and sites were in submersed macrophyte stands with representative density and height for each wetland. In the field, invertebrates for stable isotope analysis were quick frozen in vials of distilled water placed in an ice-isopropanol bath. Reference samples for gut-content analysis were preserved in 10% formalin.

Seston was collected on precombusted glass-fiber filters (Whatman GF/F or Gelman AE). To prevent contamination of seston, zooplankton were removed from samples by prefiltering through a 243- μm mesh and by carefully inspecting the residue retained by the glass-fiber filters. Epiphyton was separated from macrophytes by a shaking method (Hart and Lovvorn 2000). Macrophyte samples were shaken vigorously in a water-filled jar for 1 min, the solution decanted through a 500- μm screen, water added again, and the shaking repeated a total of three times. The water in the jar was clear after the third shaking. The three decanted solutions were pooled and three 10-mL subsamples of the pooled solution were filtered onto precombusted glass-fiber filters. The cleaned macrophytes were kept for analysis.

Sediments were collected with a plastic corer 5 cm in diameter and dried immediately upon return to the laboratory. We use the term "small sediments" for particles <100 μm sieved from the top 1–2 cm of sediments after oven drying. This fraction had very high organic content, and microscopic inspection revealed few if any vascular plant fragments. Subsequently, we used the small sediment fraction to represent the organic matter in epipelon.

Samples for $\delta^{13}\text{C}$ analysis were rinsed with 10% HCl to remove CaCO_3 precipitates; samples for $\delta^{15}\text{N}$ analysis were not acid rinsed. All samples were rinsed with distilled water before being homogenized. For amphipods (*Hyalella azteca*) and chironomid larvae (*Chironomus* spp. and Orthocladinae), gut contents were removed before isotope analysis. Most isotope measurements were made at the University of Wyoming Stable Isotope Facility using a MicroMass Isoprime continuous-flow isotope-ratio mass spectrometer (MicroMass, Manchester, UK). Precision was $\pm 0.1\%$

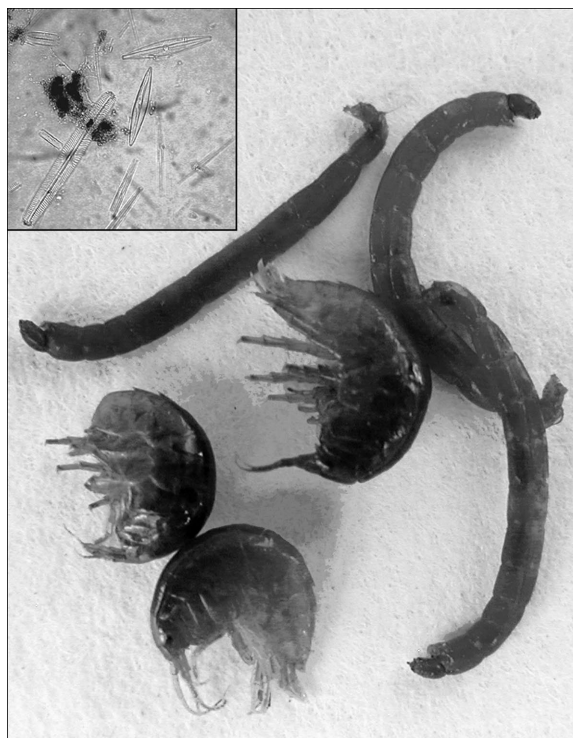


PLATE 1. Amphipods (*Hyalella azteca*), chironomid larvae, diatoms, and amorphous detritus (dark, formless material in inset) from a wetland in the Laramie Basin, Wyoming (USA). Photo by E. A. Hart.

for $\delta^{13}\text{C}$ and $\pm 0.3\%$ for $\delta^{15}\text{N}$. Some samples with particularly low nitrogen content were measured with a dual-inlet isotope-ratio mass spectrometer at The Ecosystems Center, Marine Biological Laboratory, Woods Hole, Massachusetts. When measurements were compared for the same samples between laboratories, all results were consistent.

For amphipods and chironomid larvae, the entire foregut was removed and transferred to a depression microscope slide where gut contents were separated from stomach walls. Gut contents were suspended in deionized water, filtered onto 0.45- μm membrane filters, mounted on a slide, and cleared with immersion oil. Each slide included the pooled gut contents of two to five chironomids or five to 10 amphipods. For each treatment of wetland and sampling period, three slides were analyzed for each invertebrate taxon. Slides were examined at $400\times$ magnification, and the first 50 particles found along a transect across the slide were classified and measured with an ocular micrometer. Percent mass of a food ingested was assumed equivalent to the area occupied by a given particle type as a percentage of the total area occupied by all 50 particles (Hall et al. 2000).

Gut contents were classified as vascular plant tissue, green algae, diatoms, or amorphous detritus. Both vascular plant tissue and algae have recognizable cellular

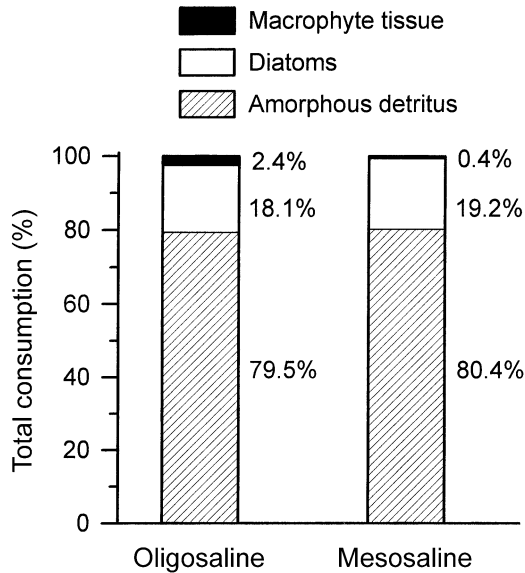


FIG. 1. Total percent mass of foods eaten by the major primary consumers (amphipods and chironomid larvae) in two oligosaline and two mesosaline wetlands in the Laramie Basin, Wyoming. Total percent mass of foods was computed as the percent mass of each food for each invertebrate taxon, weighted by that taxon's mean percentage of total invertebrate dry mass in these wetlands (Table 1). Amorphous detritus was organic particles that contained no recognizable cellular structures.

structures (e.g., rigid cell walls). We defined amorphous detritus according to Hall et al. (2000): particles with no recognizable cellular structure, which appear as discrete aggregations of subcellular-sized particles using phase-contrast microscopy. Examination of many samples indicated that diatoms comprised most of the algal community in the phytoplankton, epiphyton, and epipelon.

RESULTS

Gut contents

For the major primary consumers in oligosaline or mesosaline wetlands, vascular macrophyte tissue com-

prised 0% of the gut contents of chironomid larvae and only 0–6% for amphipods (Table 1). The highest fraction of macrophyte detritus ingested was 11% by amphipods in early June in Nelson Pond. Instead, chironomid and amphipod guts contained mainly diatoms and amorphous detritus, in terms of both frequency of occurrence and percent mass. When percent mass of each food was weighted by the percentage of total invertebrate biomass comprised by these two taxa (Table 1), ingestion patterns were very similar between wetland types (Fig. 1).

Stable isotopes

Differences between sampling periods.—For $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, the most apparent pattern was change between early June and mid-August samples (Figs. 2 and 3). Values changed in all wetlands, and there was no obvious difference in the pattern of change between oligosaline and mesosaline wetlands. Values of $\delta^{13}\text{C}$ tended to be heavier in August, while there was no clear trend for $\delta^{15}\text{N}$. On average, $\delta^{13}\text{C}$ values changed more than $\delta^{15}\text{N}$ values. Between early June and mid-August in all wetlands, $\delta^{13}\text{C}$ values changed on average by 3.5‰ for macroinvertebrate consumers; 2.1‰ for seston, epiphyton, and small sediments (epipelon); and 0.7‰ for submersed macrophytes. For $\delta^{15}\text{N}$, values changed on average by 1.1‰ for macroinvertebrate consumers; 1.4‰ for seston, epiphyton, and small sediments; and 0.4‰ for submersed macrophytes. For a particular sample type, the magnitude of seasonal change ranged from nearly 0 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of emergent plants to 8.5‰ $\delta^{13}\text{C}$ for zooplankton in Creighton Lake and 3.7‰ $\delta^{15}\text{N}$ for seston in Lake George.

Differences between wetland types.—Values of $\delta^{13}\text{C}$ in mesosaline wetlands were generally less negative (heavier or less fractionated) than in oligosaline wetlands. This pattern likely corresponded to the higher alkalinity in mesosaline than oligosaline wetlands (three to four times higher, Hart and Lovvorn 2000), and the dominance of HCO_3^- in DIC pools (Fry 1996). Although plants in saline wetlands can use HCO_3^- as

TABLE 1. Percent mass of foods in the guts of amphipods (*Hyalella azteca*) and chironomid larvae (*Chironomus* spp. or Orthocladinae) for early June and mid-August combined, dry mass of these invertebrate taxa as a percentage of the total dry mass of macroinvertebrates averaged for oligosaline vs. mesosaline lakes (Wollheim and Lovvorn 1995), and total percent mass of each food consumed by amphipods and chironomids combined.

Measure	Oligosaline						Mesosaline					
	George			Nelson			Creighton			Gibbs		
	Amphi-pods	Chironomids	Total	Amphi-pods	Chironomids	Total	Amphi-pods	Chironomids	Total	Amphi-pods	Chironomids	Total
Gut contents												
Macrophyte tissue	0	0	0	6	0	5	3	0	1	0	0	0
Diatoms	17	68	26	4	44	11	3	5	4	13	41	34
Green algae	0	3	1	0	0	0	0	0	0	0	0	0
Amorphous detritus	83	29	74	90	56	84	94	95	95	85	59	66
Invertebrate dry mass	83	17		83	17		26	74		26	74	

Notes: Total percent mass was calculated by weighting the percent mass of each food in each taxon by that taxon's percentage of total invertebrate dry mass. Amorphous detritus was organic particles with no recognizable cellular structures.

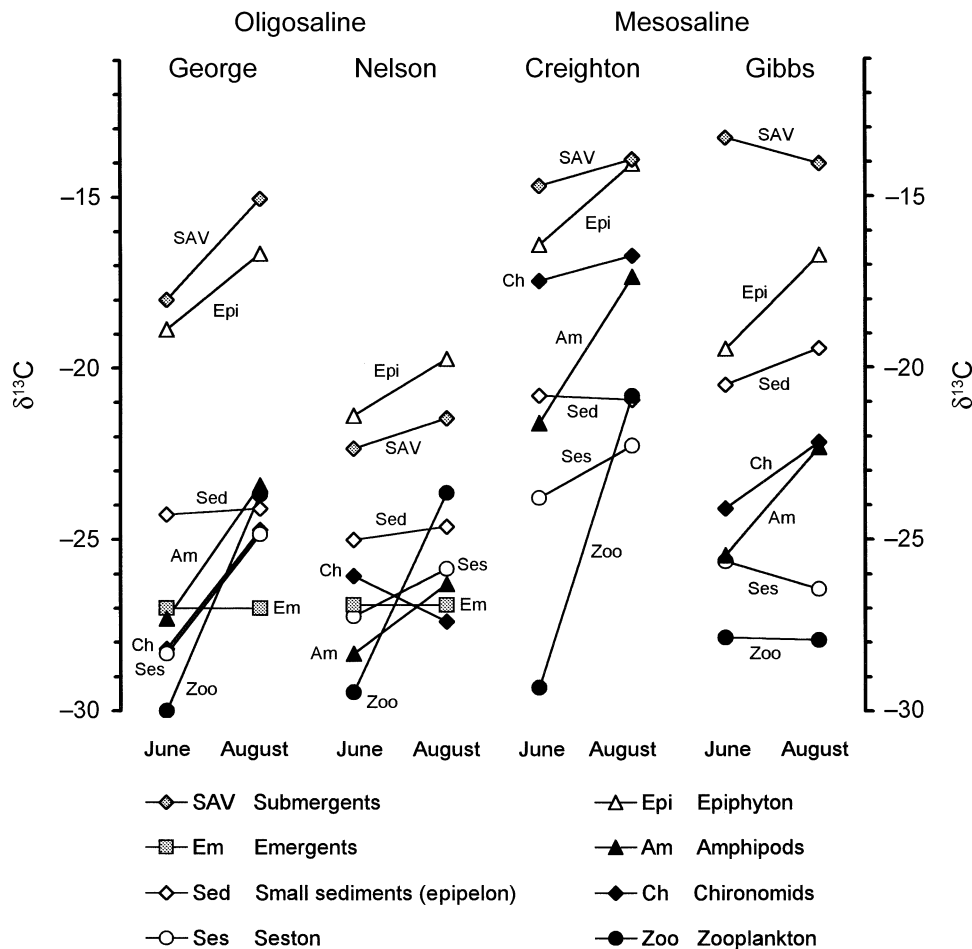


FIG. 2. Mean $\delta^{13}\text{C}$ values ($n = 3$ samples per wetland) in early June and mid-August in oligosaline wetlands George and Nelson and mesosaline wetlands Creighton and Gibbs in the Laramie Basin, Wyoming. Submersed aquatic vegetation (SAV) was *Chara* spp. in oligosaline wetlands and *Potamogeton pectinatus* in mesosaline wetlands; emergents were *Scirpus acutus*. Amphipods were *Hyalella azteca*, chironomid larvae were *Chironomus* spp. and Orthocladinae, and zooplankton were copepods (mainly *Diaptomus* spp.) and cladocerans (mainly *Daphnia* spp.). Shaded symbols are for macrophytes, open symbols for algae, and solid symbols for primary consumers. For standard deviations, see Hart (2001) or the Appendix.

a source of inorganic carbon, they prefer CO_2 (Maberly and Madsen 1998); with more CO_2 in oligosaline wetlands, plants will be more selective of the preferred light isotope. Within wetlands, $\delta^{13}\text{C}$ values were always lowest (most selection against heavy isotope) for seston and always highest (least selection against heavy isotope) for submersed macrophytes and associated epiphyton. In oligosaline wetlands, $\delta^{13}\text{C}$ of submersed macrophytes and epiphyton tended to group apart from values for emergent plants, seston, small sediments (epipelon), and consumers. In mesosaline wetlands, $\delta^{13}\text{C}$ values were more evenly distributed.

For $\delta^{15}\text{N}$, samples from mesosaline wetlands tended to have greater and more varied values than those from oligosaline wetlands. In all wetlands, $\delta^{15}\text{N}$ for organic matter in seston was greater in mid-August than in early June. Beyond this trend, few patterns in $\delta^{15}\text{N}$ were evident and we chose not to interpret results further. Effects of varying food quality (C:N ratios, Adams and

Sterner 2000), relative turnover rates at different trophic levels, and the seasonal change of $\delta^{15}\text{N}$ at the base of foodwebs rendered assumptions about trophic-level ^{15}N enrichment unreliable (Hart and Lovvorn 2002). That is, $\delta^{15}\text{N}$ could have been enriched by anywhere from 0 to 3.4‰ (or an even wider range) with each trophic level, and we had no basis for assuming a particular value.

Organic matter sources.—In oligosaline wetlands, $\delta^{13}\text{C}$ values for amphipods and chironomid larvae differed strongly from those for submersed macrophytes (*Chara*), epiphyton, and small sediments (epipelon) (Fig. 2). While gut contents of these consumers contained little or no identifiable macrophyte tissues (Table 1, Fig. 1), their $\delta^{13}\text{C}$ values overlapped those of emergent plants (*Scirpus acutus*)—emergent carbon might be incorporated into flocs or microbial biofilms and comprise a portion of amorphous detritus. However, in Lake George, chironomids ate 68% diatoms while am-

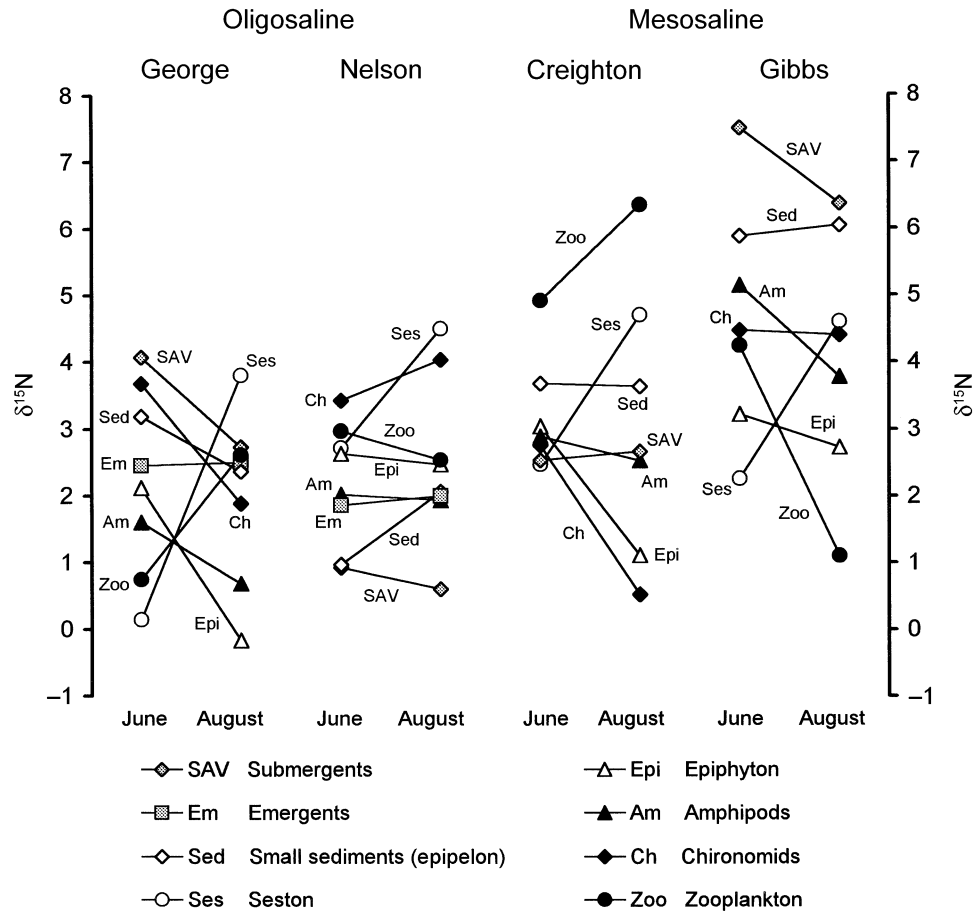


FIG. 3. Mean $\delta^{15}\text{N}$ values in early June and mid-August in oligosaline wetlands George and Nelson and mesosaline wetlands Creighton and Gibbs. Conventions are as in Fig. 2.

phipods ate only 17% diatoms (Table 1), yet their $\delta^{13}\text{C}$ values showed very similar magnitudes and seasonal trends (Fig. 2). Moreover, these values and trends differed from those for emergent plants and closely resembled those for seston. Patterns were similar in Lake Nelson for amphipods, but data for chironomids were inconclusive.

In mesosaline wetlands, $\delta^{13}\text{C}$ of amphipods and chironomid larvae varied in their similarity to organic matter sources. However, values for these consumers were much different from those for submersed macrophytes (*Potamogeton pectinatus*) and epiphyton (there were no emergents in these wetlands). Thus, as in oligosaline wetlands, strong differences in $\delta^{13}\text{C}$ between consumers and submersed macrophytes were consistent with lack of macrophyte tissue in gut contents, and suggest that microalgae were the main source of organic matter for invertebrate food webs.

DISCUSSION

Macrophyte tissue, microalgae, and amorphous detritus as food sources

Despite major differences in macrophytes and macroinvertebrates present, very little macrophyte tissue

was directly ingested by the main primary consumers in either oligosaline or mesosaline wetlands. We did not expect consumption of live tissue, but oligosaline wetlands contained abundant dead macrophyte material both from *Scirpus acutus* and *Chara* spp. In mesosaline wetlands that lacked emergent plants, submersed macrophyte stands were dense; however, availability of dead *Potamogeton pectinatus* to macroinvertebrates may be limited because much of it is washed to the shore and accumulates there as wrack. Lack of macrophyte CPOM in consumer guts indicates that the paradigm of FPOM being generated mainly by shredding macroinvertebrates does not apply to all wetland types (Wissinger 1999), and certainly not to wetlands in this study. Note that the dominant amphipod in these wetlands was *Hyalella azteca*, and *Gammarus* spp. were rare. The few *Gammarus lacustris* collected (only in Lake George) had a high fraction of *Chara* tissue in their guts.

The bulk of consumer gut contents was amorphous detritus, but many diatoms were also consumed (Fig. 1). The relative dietary (and isotopic) contribution of these two food types depends on consumer assimilation

efficiencies. Consumer uptake of carbon from diatoms and amorphous detritus would have been equal if diatom assimilation efficiency were four times that of amorphous detritus. Such a difference is possible. Macroinvertebrate assimilation efficiencies for diatoms can be as high as 90%, and those for amorphous detritus as low as 10% (50–90% for diatoms of various taxa, Wotton 1994; 10–27% for amorphous detritus in streams, Benke and Wallace 1980, 1997). However, in some cases in our study, amorphous detritus was consumed in such high fractions that it seems unlikely that most assimilated energy came directly from whole diatoms. Also, consumer assimilation efficiencies for amorphous detritus may vary widely among different systems. Specifically, the fraction of amorphous detritus derived from bacterial production is critical, as the assimilation efficiency of bacterial EPS by macroinvertebrates can exceed 80% (>80% for copepods, Decho and Moriarty 1990; 80–90% for black fly larvae, Couch et al. 1996).

We expected stable isotopes to help resolve which sources of organic matter were most important to consumers, but our experience was not completely satisfying. We originally intended to use multiple stable isotopes: ^{34}S , ^{15}N , and ^{13}C . We found that $\delta^{34}\text{S}$ values were too variable to be useful in answering our questions, e.g., with up to 30‰ difference among seston samples collected in the same wetland (cf., Neill and Cornwell 1992, Stribling and Cornwell 1997). A major cause of variation in $\delta^{34}\text{S}$ in wetlands is reduction of sulfate during bacterial respiration in anaerobic sediments, which can fractionate ^{34}S by 20–70‰ (Chambers and Trudinger 1979). Given the large vertical and horizontal variation in redox states of wetland soils (Cornwell et al. 1995), high variation of $\delta^{34}\text{S}$ in plants and consumers can confound its use in food web analyses. Also because of high variability in our wetlands, we were not comfortable applying a trophic-level enrichment factor of +3.4‰, or any other enrichment factor, to interpret $\delta^{15}\text{N}$ data (Hart and Lovvorn 2002). Thus, for inferences about organic matter sources for primary consumers and the origin of amorphous detritus, we limited our analyses to $\delta^{13}\text{C}$.

In both oligosaline and mesosaline wetlands, $\delta^{13}\text{C}$ values appeared to preclude submersed macrophytes as a carbon source for consumers. In mesosaline wetlands, exclusion of submersed macrophytes indicates that consumers rely on microalgae, the only other group of primary producers. In oligosaline wetlands, $\delta^{13}\text{C}$ of consumers changed between June and August by 1.3 to 4.4‰; since gut contents did not indicate a diet switch, this pattern requires a food source with high turnover such as microalgae. However, even with no macrophyte tissue in gut contents, it is still possible that emergent macrophytes contributed to consumer diets if amorphous detritus contained a high fraction of assimilable emergent carbon. This situation could occur if amorphous detritus contained assimilable flocs

of DOM produced by emergent macrophytes, or contained EPS from bacteria that had consumed such flocs or had directly consumed emergent macrophyte tissue (Gallagher et al. 1976, Camilleri and Ribí 1986, Alber and Valiela 1995, 1996, Mann and Wetzel 1996). Diatoms dominated the epipelton and epiphyton in our wetlands (Hart 1998), and in some systems diatom-rich biofilms can exude up to 73% of carbon fixed depending on growth phase (Goto et al. 1999). In contrast, exudation of DOM by vascular macrophytes and macroalgae is generally <12% of carbon fixed and usually <5% (Brylinsky 1977, Søndergaard 1981, Pregall 1983, Moriarty et al. 1986). Based on relative primary production of labile extracellular material, it is more likely that bacterial production during our study was based mainly on algal exudates and algal detritus (Søndergaard et al. 1995). We conclude that in both oligosaline and mesosaline wetlands, food webs were based mainly on microalgae.

Nature of amorphous detritus

In our study, macroinvertebrate gut contents were mostly amorphous detritus. In oligosaline wetlands, amphipods that ate mainly amorphous detritus but some diatoms, and chironomids that ate a much higher fraction of diatoms, had similar $\delta^{13}\text{C}$ values. This result suggests either (1) that consumer assimilation efficiency of diatoms was much greater than that of amorphous detritus (see *Discussion: Macrophyte tissue, microalgae, and amorphous detritus as food sources*), or (2) that most carbon in amorphous detritus was originally fixed by diatoms. If amorphous detritus were assimilated with low efficiency, one would expect it to be largely recalcitrant material of macrophyte origin. However, inspection of gut contents revealed no cellular structures, and the substance was sticky and slime-like (cf., Engel 2000). Much of the amorphous detritus in chironomid and amphipod guts retained Alcian blue stain; this staining indicates muco-polysaccharides, the main component of microbial EPS (Passow and Alldredge 1995). These aspects support case (2) that most amorphous detritus was extracellular material derived from algal photosynthesis, including flocculated DOM and surface-bound EPS.

Understanding the nature of amorphous detritus and DOM/EPS is a central issue for future research in wetlands. It will be difficult to understand the trophic dynamics of macroinvertebrates without knowing the assimilation efficiency of amorphous detritus vs. other foods. Also, if amorphous detritus is highly assimilable (e.g., DOM/EPS) then standard measures of microalgae and bacteria will not reflect their trophic importance: extracellular production may be poorly represented by traditional measures such as cell counts, chlorophyll *a*, and tracer incorporation into cells. Because amorphous detritus is probably an important component of macroinvertebrate diets in most wetlands (e.g., Johnson et al. 2000), we suggest that characterizing its nature

among wetland types (e.g., prairie vs. forested wetlands) and under different conditions (e.g., wet and dry cycles) will be key to understanding patterns of secondary production in wetlands.

Importance of different microalgal types

If microalgae are the trophic base of food webs in these wetlands, one might expect production by different invertebrate groups to be linked to production by different forms of microalgae (Goldsborough and Robinson 1996). That is, in oligosaline wetlands where most algal production is in epiphyton, epiphytic grazers (amphipods) would dominate invertebrate biomass. In mesosaline wetlands where phytoplankton and epipelton are more productive, filter-feeding zooplankton and deposit-feeding chironomid larvae would be more abundant. In several cases, the carbon isotope data appeared to contradict a direct link between forms of macroinvertebrate production and forms of microalgal production. For example, in oligosaline wetlands where most algal biomass and production was epiphytic (Hart and Lovvorn 2000), $\delta^{13}\text{C}$ values for *Hyalella azteca* and chironomid larvae differed by 5 to 9‰ from that for epiphyton. The $\delta^{13}\text{C}$ signal for epiphyton was surprisingly absent in macroinvertebrates, whose values were most similar to seston (Fig. 2).

If production by epiphyton is so high in these wetlands, then why is its $\delta^{13}\text{C}$ signal so weak in primary consumers? The $\delta^{13}\text{C}$ data may rightly indicate that planktonic processes are much more important to consumers than expected from the biomass and production of different algal types, in which the contribution by phytoplankton was relatively small (Hart and Lovvorn 2000). Epiphytic chironomid larvae might mainly filter feed on seston, but amorphous detritus in the guts of *Hyalella azteca* probably came from feeding on surfaces (epipelton or epiphyton). A possible explanation is that epiphytic carbon assimilated by consumers does not reflect the $\delta^{13}\text{C}$ of bulk epiphyton as we measured it. Similarity in $\delta^{13}\text{C}$ of epiphyton and macrophyte hosts (Fig. 2) suggests that macrophytes influenced the $\delta^{13}\text{C}$ of epiphyton. In these wetlands, particularly on *Chara* spp., epiphyton was very dense. Algae in the inner layers of epiphyton (nearest leaf surfaces) may incorporate CO_2 produced by respiration of organic matter fixed by the macrophyte host: either DOC leaked from the macrophyte and respired by microbes to yield CO_2 , or else leaked DIC (CO_2) produced by respiration within the macrophyte. In contrast, algae in the outer layers of epiphyton would be exposed to the different inorganic carbon pool used by algae in the seston. Amphipods and chironomids might graze mainly the outer layers of epiphyton (Steinman 1996), explaining why their $\delta^{13}\text{C}$ values resemble that of seston. Also, the outer layers of epiphyton might be a repository for planktonic production: microalgae and DOM/EPS released in the water column may flocculate into "wetland snow" (sensu Grossart et al. 1997) that settles on surfaces of

submersed macrophytes. Resolving these issues will be key to tracing the relative roles of phytoplankton and periphyton in food web dynamics (Golsborough and Robinson 1996, Goto et al. 1999, 2001), and ensuring that contributions by macrophytes are distinguished from those of epiphytes growing on them (cf., Reitner et al. 1999, Ziegler and Benner 1999).

Conclusions

In saline wetlands of Wyoming, there was almost no direct ingestion of macrophyte tissue by dominant primary consumers. Guts contained some diatoms but mostly amorphous detritus. Patterns of $\delta^{13}\text{C}$ at different times yielded strong inference that microalgae were the ultimate source of organic matter for macroinvertebrates. Thus, the traditional paradigm that wetland food webs are based mainly on decomposing macrophyte tissue does not apply to these wetlands and probably many others. Our results suggest that characterizing the nature of amorphous detritus (origins, production patterns, nutritional value) will be important to understanding macroinvertebrate production and food web structure in a broad range of wetland types.

ACKNOWLEDGMENTS

This research was supported by an Edward D. and Sally M. Futch Graduate Fellowship from the Institute for Wetland and Waterfowl Research of Ducks Unlimited, the Delta Waterfowl and Wetlands Research Station, and the Wyoming Water Resources Center. We thank J. M. Welker, R. M. Larson, and M. Otter for assistance with stable isotope analyses, and R. O. Hall, J. S. Meyer, C. Martinez del Rio, and W. A. Reiners for helpful comments on the manuscript.

LITERATURE CITED

- Adams, T. S., and R. W. Sterner. 2000. The effect of dietary nitrogen content on trophic level ^{15}N enrichment. *Limnology and Oceanography* **45**:601–607.
- Alber, M., and I. Valiela. 1995. Organic aggregates in detrital food webs: incorporation by bay scallops *Argopecten irradians*. *Marine Ecology Progress Series* **121**:117–124.
- Alber, M., and I. Valiela. 1996. Utilization of microbial organic aggregates by bay scallops, *Argopecten irradians* (Lamarck). *Journal of Experimental Marine Biology and Ecology* **195**:71–89.
- Barlocher, F., and N. R. Biddiscombe. 1996. Geratology and decomposition of *Typha latifolia* and *Lythrum salicaria* in a freshwater marsh. *Archiv für Hydrobiologie* **136**:309–325.
- Batzer, D. P., and S. A. Wissinger. 1996. Ecology of insect communities in non-tidal wetlands. *Annual Review of Entomology* **41**:75–100.
- Benke, A. C., and J. B. Wallace. 1980. Trophic basis of production among net-spinning caddisflies in a southern Appalachian stream. *Ecology* **61**:108–118.
- Benke, A. C., and J. B. Wallace. 1997. Trophic basis of production among riverine caddisflies: implications for food web analysis. *Ecology* **78**:1132–1145.
- Boschker, H. T. S., E. M. J. Dekkers, R. Pel, and T. E. Capenberg. 1995. Sources of organic carbon in the littoral of Lake Gooimeer as indicated by stable carbon isotope and carbohydrate compositions. *Biogeochemistry* **29**:89–105.
- Brylinsky, M. 1977. Release of dissolved organic matter by some marine macrophytes. *Marine Biology* **39**:213–220.
- Camilleri, J. C., and G. Ribí. 1986. Leaching of dissolved organic carbon (DOC) from dead leaves, formation of

- flakes from DOC, and feeding on flakes by crustaceans in mangroves. *Marine Biology* **91**:337–344.
- Campeau, S., H. R. Murkin, and R. D. Titman. 1994. Relative importance of algae and emergent plant litter to freshwater macroinvertebrates. *Canadian Journal of Fisheries and Aquatic Sciences* **51**:681–692.
- Chambers, L. A., and P. A. Trudinger. 1979. Microbiological fractionation of stable sulfur isotopes: a review and critique. *Geomicrobiology Journal* **1**:249–293.
- Cornwell, J. C., C. Neill, and J. C. Stevenson. 1995. Biogeochemical origin of $\delta^{34}\text{S}$ isotopic signatures in a prairie marsh. *Canadian Journal of Fisheries and Aquatic Sciences* **52**:1816–1820.
- Couch, C. A., J. L. Meyer, and R. O. Hall. 1996. Incorporation of bacterial extracellular polysaccharide by black fly larvae (Simuliidae). *Journal of the North American Benthological Society* **15**:289–299.
- Cuffney, T. F., J. B. Wallace, and G. J. Lughart. 1990. Experimental evidence quantifying the role of benthic invertebrates in organic matter dynamics of headwater streams. *Freshwater Biology* **23**:281–299.
- Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry, and W. B. Taliaferro. 1989. Shredders and riparian vegetation. *BioScience* **39**:24–30.
- Currin, C. A., S. Y. Newell, and W. W. Paerl. 1995. The role of standing dead *Spartina alterniflora* and benthic microalgae in salt marsh food webs: considerations based on multiple stable isotope analysis. *Marine Ecology Progress Series* **121**:99–116.
- Decho, A. W. 1990. Microbial exopolymer secretions in ocean environments: their role(s) in food webs and marine processes. *Oceanography and Marine Biology Annual Review* **28**:73–153.
- Decho, A. W., and D. J. W. Moriarty. 1990. Bacterial exopolymer utilization by a harpacticoid copepod: a methodology and results. *Limnology and Oceanography* **35**:1039–1049.
- de Szalay, F. A., and V. H. Resh. 1996. Spatial and temporary variability of trophic relationships among aquatic macroinvertebrates in a seasonal marsh. *Wetlands* **16**:458–466.
- Engel, A. 2000. The role of transparent exopolymer particles (TEP) in the increase in apparent particle stickiness (α) during the decline of a diatom bloom. *Journal of Plankton Research* **22**:485–497.
- Euliss, N. H., D. A. Wrubleski, and D. M. Mushet. 1999. Wetlands of the prairie pothole region: invertebrate species composition, ecology, and management. Pages 471–514 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America: ecology and management*. Wiley, New York, New York, USA.
- Fry, B. 1991. Stable isotope diagrams of freshwater food webs. *Ecology* **72**:2293–2297.
- Fry, B. 1996. $^{13}\text{C}/^{12}\text{C}$ fractionation by marine diatoms. *Marine Ecology Progress Series* **134**:283–294.
- Gallagher, J. L., W. J. Pfeiffer, and L. R. Pomeroy. 1976. Leaching and microbial utilization of dissolved organic carbon from leaves of *Spartina alterniflora*. *Estuarine, Coastal and Shelf Science* **4**:467–471.
- Goldsborough, L. G., and G. G. C. Robinson. 1996. Pattern in wetlands. Pages 77–117 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe, editors. *Algal ecology: freshwater benthic ecosystems*. Academic Press, New York, New York, USA.
- Goto, N., T. Kawamura, O. Mitamura, and H. Terai. 1999. Importance of extracellular organic carbon production in the total primary production by tidal-flat diatoms in comparison to phytoplankton. *Marine Ecology Progress Series* **190**:289–295.
- Goto, N., O. Mitamura, and H. Terai. 2001. Biodegradation of photosynthetically produced extracellular organic carbon from intertidal benthic algae. *Journal of Experimental Marine Biology and Ecology* **257**:73–86.
- Grossart, H.-P., M. Simon, and B. E. Logan. 1997. Formation of macroscopic aggregates (lake snow) in a large lake: the significance of transparent exopolymer particles, phytoplankton, and zooplankton. *Limnology and Oceanography* **42**:1651–1659.
- Hall, R. O., J. B. Wallace, and S. L. Eggert. 2000. Organic matter flow in stream food webs with reduced detrital resource base. *Ecology* **81**:3445–3463.
- Hammer, D. A. 1997. *Creating freshwater wetlands*. Second edition. CRC Press/Lewis Publishers, Boca Raton, Florida, USA.
- Hart, E. A. 1998. Primary production in saline wetlands of the Laramie Basin. Thesis. University of Wyoming, Laramie, Wyoming, USA.
- Hart, E. A. 2001. Macroinvertebrate foodwebs in saline wetlands of the Laramie Basin. Dissertation. University of Wyoming, Laramie, Wyoming, USA.
- Hart, E. A., and J. R. Lovvorn. 2000. Vegetation dynamics and primary production in saline, lacustrine wetlands of a Rocky Mountain basin. *Aquatic Botany* **66**:21–39.
- Hart, E. A., and J. R. Lovvorn. 2002. Interpreting stable isotopes from macroinvertebrate foodwebs in saline wetlands. *Limnology and Oceanography* **47**:580–584.
- Horne, A. J., and C. R. Goldman. 1994. *Limnology*. Second edition. McGraw Hill, New York, New York, USA.
- Johnson, B. R., D. C. Tarter, and J. J. Hutchens. 2000. Life history and trophic basis of production of the mayfly *Calibaetis fluctuans* (Walsh) (Ephemeroptera: Baetidae) in a mitigated wetland, West Virginia, USA. *Wetlands* **20**:397–405.
- Kwak, T. J., and J. B. Zedler. 1997. Food web analysis of southern California coastal wetlands using multiple stable isotopes. *Oecologia* **110**:262–277.
- Lovvorn, J. R., W. M. Wollheim, and E. A. Hart. 1999. High Plains wetlands of southeast Wyoming: salinity, vegetation, and invertebrate communities. Pages 603–633 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America: ecology and management*. Wiley, New York, New York, USA.
- Maberly, S. C., and T. V. Madsen. 1998. Affinity for CO_2 in relation to the ability of freshwater macrophytes to use HCO_3^- . *Functional Ecology* **12**:99–106.
- Mann, C. J., and R. G. Wetzel. 1996. Loading and utilization of dissolved organic carbon from emergent macrophytes. *Aquatic Botany* **53**:61–71.
- Mann, K. H. 1988. Production and use of detritus in various freshwater, estuarine, and coastal ecosystems. *Limnology and Oceanography* **33**:910–930.
- Marble, A. D. 1992. *A guide to wetland functional design*. Lewis Publishers, Chelsea, Michigan, USA.
- Mihuc, T., and D. Toetz. 1994. Determination of diets of alpine aquatic insects using stable isotopes and gut contents. *American Midland Naturalist* **131**:146–155.
- Mitsch, W. J., and J. G. Gosselink. 2000. *Wetlands*. Third edition. Van Nostrand Reinhold, New York, New York, USA.
- Moriarty, D. J. W., R. L. Iverson, and P. C. Pollard. 1986. Exudation of organic carbon by the seagrass *Halodule wrightii* Aschers. and its effect on bacterial growth in the sediment. *Journal of Experimental Marine Biology and Ecology* **96**:115–126.
- Murkin, H. R. 1989. The basis for food chains in prairie wetlands. Pages 316–338 in A. G. van der Valk, editor. *Northern prairie wetlands*. Iowa State University Press, Ames, Iowa, USA.

- Neill, C., and J. C. Cornwell. 1992. Stable carbon, nitrogen, and sulfur isotopes in a prairie marsh food web. *Wetlands* **12**:217–224.
- Newell, S. Y., M. A. Moran, R. Wicks, and R. E. Hodson. 1995. Productivities of microbial decomposers during early stages of decomposition of leaves of a freshwater sedge. *Freshwater Biology* **34**:135–148.
- Page, H. M. 1997. Importance of vascular plant and algal production to macro-invertebrate consumers in a southern California salt marsh. *Estuarine, Coastal and Shelf Science* **45**:823–834.
- Passow, U., and A. L. Alldredge. 1995. A dye-binding assay for the spectrophotometric measurement of transparent exopolymer particles (TEP). *Limnology and Oceanography* **40**:1326–1335.
- Peck, D. E., and J. R. Lovvorn. 2001. The importance of flood irrigation in water supply to wetlands in the Laramie Basin, Wyoming, USA. *Wetlands* **21**:370–378.
- Pregnall, A. M. 1983. Release of dissolved organic carbon from the estuarine intertidal macroalga *Enteromorpha prolifera*. *Marine Biology* **73**:37–42.
- Reitner, B., A. Herzig, and G. H. Herndl. 1999. Dynamics in bacterioplankton production in a shallow, temperate lake (Lake Neusiedl, Austria): evidence for dependence on macrophyte production rather than on phytoplankton. *Aquatic Microbial Ecology* **19**:245–254.
- Robinson, G. G. C., S. E. Gurney, and L. G. Goldsborough. 1997. The primary productivity of benthic and planktonic algae in a prairie wetland under controlled water-level regimes. *Wetlands* **17**:182–194.
- Søndergaard, M. 1981. Kinetics of extracellular release of ^{14}C -labelled organic carbon by submerged macrophytes. *Oikos* **36**:331–347.
- Søndergaard, M., B. Hansen, and S. Markager. 1995. Dynamics of dissolved organic carbon lability in a eutrophic lake. *Limnology and Oceanography* **40**:46–54.
- Steinman, A. D. 1996. Effects of grazers on freshwater benthic algae. Pages 341–373 in R. J. Stevenson, M. L. Bothwell, and R. L. Lowe, editors. *Algal ecology: freshwater benthic ecosystems*. Academic Press, New York, New York, USA.
- Stribling, J. M., and J. C. Cornwell. 1997. Identification of important primary producers in a Chesapeake Bay tidal creek system using stable isotopes of carbon and sulfur. *Estuaries* **20**:77–85.
- Vander Zanden, M. J., and J. B. Rasmussen. 2001. Variation in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ trophic fractionation: implications for aquatic food web studies. *Limnology and Oceanography* **46**:2061–2066.
- Webster, J. R., and E. F. Benfield. 1986. Vascular plant breakdown in freshwater ecosystems. *Annual Review of Ecology and Systematics* **17**:567–594.
- Wissinger, S. A. 1999. Ecology of wetland invertebrates: synthesis and applications for conservation and management. Pages 1043–1086 in D. P. Batzer, R. B. Rader, and S. A. Wissinger, editors. *Invertebrates in freshwater wetlands of North America*. Wiley, New York, New York, USA.
- Wollheim, W. M., and J. R. Lovvorn. 1995. Salinity effects on macroinvertebrate assemblages and waterbird food webs in shallow lakes of the Wyoming High Plains. *Hydrobiologia* **310**:207–223.
- Wollheim, W. M., and J. R. Lovvorn. 1996. Effects of macrophyte growth forms on invertebrate communities in saline lakes of the Wyoming High Plains. *Hydrobiologia* **323**:83–96.
- Wotton, R. S. 1994. Particulate and dissolved organic matter as food. Pages 235–288 in R. S. Wotton, editor. *The biology of particles in aquatic ecosystems*. Lewis Publishers, Boca Raton, Florida, USA.
- Ziegler, S., and R. Benner. 1999. Dissolved organic carbon cycling in a subtropical seagrass-dominated lagoon. *Marine Ecology Progress Series* **180**:149–160.

APPENDIX

Tables of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values are available in ESA's Electronic Data Archive: *Ecological Archives* E084-090-A1.